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DIMORPHISM OF THE METASTERNAL WINGS IN *AGABUS RAFFRAYI* SHARP AND *A. LABIATUS* BRAHM (COL., DYTISCIDAE) AND ITS RELATION TO CAPACITY FOR FLIGHT.

By Dorothy J. Jackson, F.R.E.S., F.L.S.

In the genus *Agabus* the shape of the metasternal wings, the side pieces of the metasternum, has been used for separating species (Fowler, 1887 ; F. Balfour-Browne, 1950) or even subgenera (Guignot, 1951 ; Zimmermann, 1934 ; and others). It is, therefore, of importance to record that in two species, *A. raffrayi* Sharp and *A. labiatus* Brahm, a dimorphism has been observed in the shape of these wings, and in *A. raffrayi* the specimens with wide metasternal wings had a fully developed flying apparatus while those with narrow metasternal wings were flightless.

Dr. Hugh Scott (1953) recorded finding *A. raffrayi* out of water on Mount Damota, in Abyssinia, on a hot bright day. I was curious to know if this species was capable of flight. At Dr. Scott's suggestion Mr. J. Balfour-Browne kindly sent me two of Dr. Scott's specimens to dissect, but they were from another locality—Mount Gughé—which Dr. Scott informs me is over 50 miles distant from Mount Damota. Both had narrow metasternal wings and dissection proved them to be flightless. A few specimens were then sent me from Mount Damota and these had wide metasternal wings and a fully developed flying apparatus. It occurred to me that two species might be involved, but on consulting Mr. J. Balfour-Browne he informed me that an examination of Dr. Scott's material showed that the aedeagus of the wide and narrow winged form were indistinguishable, and this I also observed later in the specimens sent me.

Mrs. Omer-Cooper (1931) described the form of *A. raffrayi* with narrow metasternal wings as a new species, *pallidus*. It is evidently only a flightless form of *raffrayi* and therefore Mr. Balfour-Browne considers that *pallidus* O.-C. falls as a synonym of *raffrayi* Sharp.

Agabus labiatus Brahm is a species characterised by narrow metasternal wings, but amongst some typical specimens kindly sent me by Prof. C. H. Lindroth from Sweden were two with wide metasternal wings. These specimens have been examined by Mr. Balfour-Browne and confirmed as *A. labiatus*.

I am much indebted to Mr. Balfour-Browne for determining these specimens and I greatly appreciate his and Dr. Scott's help in supplying me with much of the material on which this paper is based. Other valuable specimens have been received from Dr. F. Guignot and Dr. F. N. Young.

Agabus raffrayi Sharp.

According to Mrs. Omer-Cooper (1931), this species is known in East Africa from Abyssinia (types), Uganda, Kenya and Tanganyika, and it is also recorded from South Africa. She records " *pallidus* " O.-C. as taken between Addis Ababa and Addis Alem, but two specimens sent me from the Omer-Cooper collection, taken at Wouramboulchi, Abyssinia, in 1926, have narrow metasternal wings, though named by Mrs. Omer-Cooper as *A. raffrayi* Sharp. However, Mr. Balfour-Browne informs me that, amongst other specimens from the same collection, there are three with the broad metasternal wings, so this affords proof that both forms may occur in the same locality.

Apart from the difference in the metasternal wings, I find the two forms of *raffrayi* indistinguishable externally, with elytra closed.[1] The colour varies in both forms from light chestnut to dark brown, and the size varies from 7·3 mm. to 8 mm. (see Table I). This species, as noted by Mrs. Omer-Cooper, has a strong resemblance to *A. paludosus* Fab., but the aedeagus is entirely different, having a double apex in *raffrayi*, while in *paludosus* the apex is single and truncated.

Material Used

Ten specimens have been sent me for study. Of these only three have wide metasternal wings and they were collected by Dr. Scott at an elevation of 10,000 ft. on Mount Damota in Wolamo Province on 5.xi.48. They are some of those he referred to (1952 : 135, and 1953) as occurring in cushions of wet moss on a rock-face over which a film of water flowed down into a pool below. The specimens with narrow metasternal wings came from two localities, five taken by Dr. Scott in a small marsh at an elevation of 11,000 ft. on Mount Gughé, in Gamo Province, on 21.xii.1948, and the two already mentioned collected at Wouramboulchi by Mr. Omer-Cooper at about 9,000 ft. on 2–7.x.1926.

All the specimens were received set on cards. I removed them to alcohol and most of them were left soaking in this for over a year, with the result that the dried muscles have regained their normal shape and are almost in as good condition as specimens preserved in alcohol since capture. Permanent mounts were made of the various parts of the metathorax in euparal or polyvinyl lactophenol, and the wings and elytra were also mounted for comparative measurements. The wings were sometimes mounted attached to the metatergum, but they were more easy to unfold if cut off at the base and transferred from alcohol to a thin smear of glycerine on a slide. They were placed dorsal side downwards, unfolded in a minimum of fluid so that the dorsal surface adhered to the slide, and then mounted direct in polyvinyl lactophenol. The wings and elytra were measured with an eyepiece micrometer and the whole beetles were measured on a millimeter scale. A low power objective on a dissecting microscope was used in taking the measurements. The wings were measured from the base of the costa to the tip, and the elytra from the base of the peduncle to the apex. All figures have been drawn with the help of a camera lucida.

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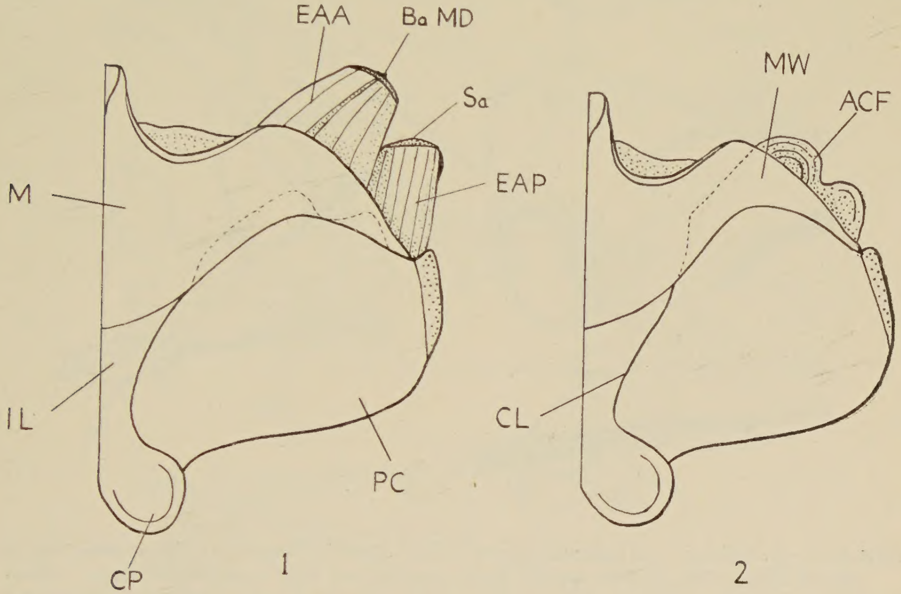
[1] Dr. F. Guignot informs me (*in litt.*) that he finds a difference between *A. raffrayi* and *A. pallidus* in the form of the meshes of the elytral reticulation. I have, therefore, made camera lucida drawings of the reticulation from several specimens of both forms, but I am unable to detect any difference. The meshes show variation in average size in the different specimens of both forms. The largest meshes occur in a soft specimen with narrow metasternal wings, but meshes of nearly the same size were found in a hard specimen with wide metasternal wings, while in other specimens of both forms the meshes are much smaller.

Comparison of the two forms of *A. raffrayi.*

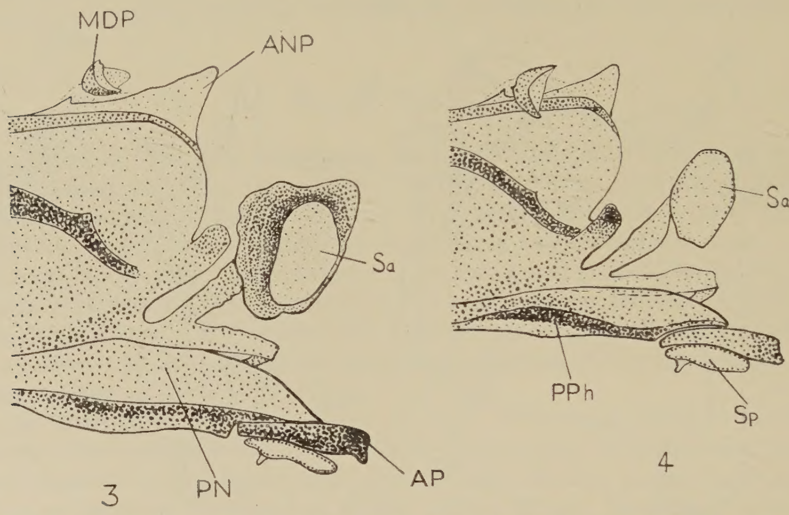
Metathorax.—The difference in shape of the metasternal wing in the two forms (figs. 1 and 2) is correlated with a difference in the shape of the post-coxa which is more produced anteriorly in the flightless form. A further difference is evident on dissection in regard to the development of an apodeme, the anterior coxal fold. This is the projecting shelf-like apodeme which gives attachment to the anterior ends of the inner group of the flexor trochanter muscles of the hind leg. In the form with narrow metasternal wings there are no fibrous flight muscles, and, on removing the met-episternum, one sees the two lobes of the anterior coxal fold projecting in front beyond the metasternal wing, (fig. 2, *ACF*). The thin, fringe-like group of short tubular muscles arising from the anterior edge of the metasternal wing immediately above the lobes (in ventral view) is not shown in the figures but is the *musculus expirator metathoracis* of Bauer (1910). In the form with broad metasternal wings the removal of the met-episternum reveals the anterior ends of the well developed pleural flight muscles (fig. 1, *EAA*, *EAP*), but the anterior coxal fold, which is much shorter, does not show at all externally and is indicated by dotted lines in fig. 1. The flexor trochanter muscles are accordingly shorter in this form and there seems little



Figs. 1–2.—(1) *Agabus raffrayi* Sharp. External view of left half of metasternum and post-coxa of male (No. 5) with normal flight muscles. From Mount Damota, Abyssinia. × 21·6. The met-episternum has been removed, exposing the upper portion of the pleural flight muscles. The anterior coxal fold is indicated by a dotted line. (2) *A. raffrayi* (*pallidus* Omer-Cooper). External view of left half of metasternum and post-coxa of male (No. 4) without flight muscles. From Mount Gughé, Abyssinia. × 21·6. The met-episternum has been removed, exposing the upper part of the anterior coxal fold; the basal part of this fold is indicated by a dotted line.

doubt that full development of the flight muscles is correlated in this species with reduced development of the flexor muscles of the hind leg.

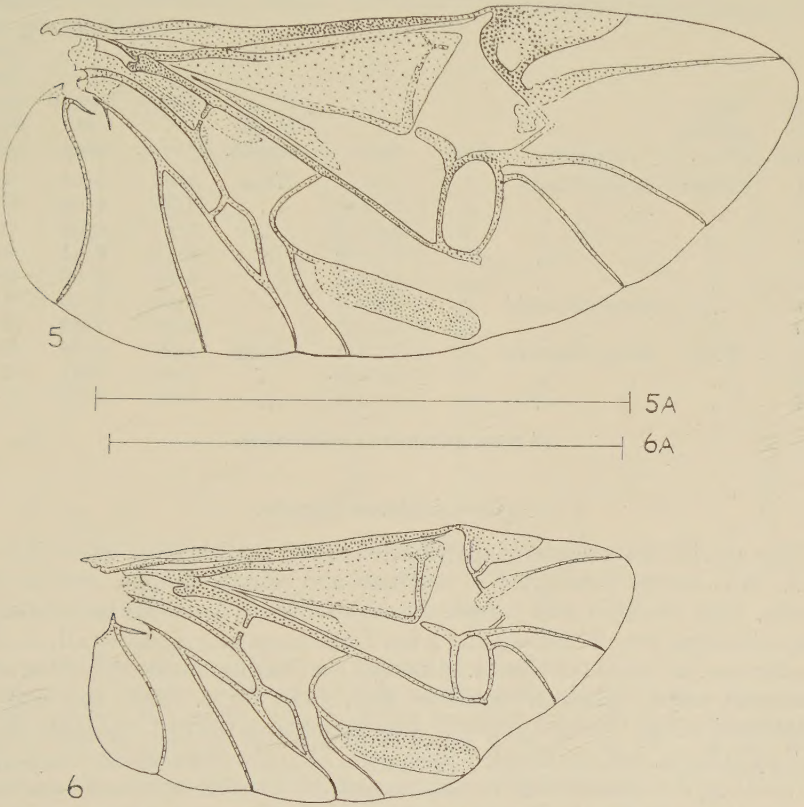
Other differences between the two forms occur in the metatergum. While it is darkly sclerotic with blue iridescence in all the (hard) specimens examined, it shows similar modifications of structure in the flightless form as have already been described in various flightless species (Jackson, 1952). Thus it is shorter from prescutum to postnotum and the prephragma and postphragma are less developed than in the form with normal flight muscles. The lateral area of the postphragma on its posterior side serves for the attachment of a short tubular muscle going to the furca (the *musculus furco-dorsalis* of Bauer, 1910), so this area of the postphragma is still prominent in the flightless beetle (fig. 4, PPh). In the form with normal flight muscles the anterior surface of the lateral area of the postphragma supports (together with the widened postnotum) the posterior ends of the oblique longitudinal flight muscles, while the median longitudinal flight muscles extend from the prephragma to the median area of the postphragma.



Figs. 3–4.—*A. raffrayi*. (3) Internal view of lateral area of metatergum with subalar disc in situ of female (No. 3) with normal flight muscles and wide metasternal wings. From Mount Damota. × 31·6. The lateral area of postnotum and post-phragma is flattened out to show the anterior surface on which the lateral oblique dorsal flight muscles are inserted. (4) Internal view of lateral area of metatergum and subalar disc of male (No. 4) without flight muscles and with narrow metasternal wings. From Mount Gughé. × 31·6. The lateral area of the postphragma is not flattened down and so the posterior edge is exposed at PPh. In this, and in the preceding figure, the thin membrane connecting the metatergum with the adjoining parts of the exoskeleton has not been represented; and the strength of the sclerotization is indicated by shading.

The discs of the pleural flight muscles, the basalar and subalar discs, show a striking difference in size in the two forms, and the subalar disc is shown in figs. 3 and 4, *Sa*.

Wings.—The difference in size of the wings in the two forms is usually evident on removing the elytra. In the flightless form the folded wings do not always reach the propygidium, while in the form with normal flight muscles they extend to the pygidium. In both forms the wings show some variation in size (Table I). In the form with wide metasternal wings, the flying wings (fig. 5) are much larger than in the flightless form, (fig. 6), but it is of interest to find that in the two flightless specimens from Wouramboulchi—which occurred in the same locality as specimens with wide metasternal wings—the length of the wings is intermediate.



Figs. 5–6.—*A. raffrayi.* (5) Wing of female (No. 3) with normal flight muscles and wide metasternal wings. From Mount Damota. × 11·8. The length of elytron at same scale is shown at 5A. (6) Wing of male (No. 2) with narrow metasternal wings and no flight muscles. From Mount Gughé. × 11·8. The length of elytron at same scale is shown at **6A.**

Flight muscles.—These are very well developed in the three specimens from Mount Damota, but they do not show at all in the other specimens, though the tubular muscles, such as the leg muscles, are well preserved.

Soft Specimen.—Only one of the ten specimens was soft. It was a female (No. 10 of Table I) with narrow metasternal wings, from Mount Gughé. It was evidently quite newly emerged as the cuticle was semi-transparent. No trace of flight muscles was found, though in teneral specimens of good flying species the flight muscles are well developed. The subalar disc was only a little smaller than in a hardened flightless form, but the anterior coxal fold was very small, not projecting beyond the metasternal wing. This has been observed in other soft examples of flightless beetles, and the apodeme must develop fully after the beetle has emerged.

TABLE I.—*Wing length compared with elytral length in specimens of* Agabus raffrayi *Sharp with narrow and with wide metasternal wings.*

Reference number.	Metasternal wings.	Locality.	Sex.	Size.	Flight muscles.	Length of elytron.	Length of wing.	Amount by which wing length exceeds elytral length.
1	Narrow	Mount Gughé	♀	7·3	None	5·36	5·83	0·47
8	,,	,, ,,	♂	7·7×4·0	,,	5·41	6·04	0·63
2	,,	,, ,,	♂	7·5×4·5	,,	5·47	6·04	0·57
10	,,	,, ,,	♀	7·7×4·0	,,	5·78	6·41	0·63
4	,,	,, ,,	♂	7·8×4·1	,,	6·04	6·83	0·79
7	,,	Wouramboulchi	♀	7·7×4·3	,,	6·04	7·10	1·06
9	,,	,,	♀	8·0×4·2	,,	6·13	7·62	1·49
6	Wide	Mount Damota	♂	7·7×4·1	Normal	5·94	8·04	2·10
3	,,	,, ,,	♀	7·8×4·2	,,	6·04	8·41	2·37
5	,,	,, ,,	♂	8·0×4·1	,,	6·31	8·41	2·10

All measurements in millimetres.

Agabus labiatus BRAHM.

This species has a scattered distribution in the British Isles, where it is very local. It is widely distributed in northern and central Europe, and occurs in Siberia. Only the form with narrow metasternal wings has so far been described. I have dissected over 40 British and a few Danish specimens and, in all, the flight muscles were abnormal or absent. Amongst six Swedish specimens, all of a light testaceous colour, taken in Skåne in May, 1880, by C. Roth, two had wide metasternal wings. These specimens were larger than the rest, the male measuring 7 by 3·8 mm. and the female 7 by 4 mm. The other Swedish specimens (with the usual type of metasternal wings) measured 6·1 to 6·2 mm., and two which I dissected were flightless. Fowler (1887) gives the size of *A. labiatus* as 6 by 3½ mm., and these two specimens with wide metasternal wings are larger than any I have seen.

Mr. Balfour-Browne informs me that Dr. Brinck has examined the collections at Lund, Sweden, and, though no specimens were present from Skåne (Scania), there were 25 from other Swedish provinces, but all these have the usual narrow metasternal wings. Through the kindness of Mr. W. Hellén and Dr. W. Hackman, I have been sent on loan 12 specimens from the Helsinki Museum, partly taken in North Finland and partly in the Åland Islands, but all are of the usual form. Eleven specimens which I collected in southwest Denmark (Lönne) are similar. The form with wide metasternal wings would, therefore, appear to be very rare. I presented one specimen, the male, to the British Museum (Natural History) and the other I dissected.

Description of the form with wide metasternal wings.

The external view of the metasternum and adjacent parts is shown in fig. 8 and the normal form in fig. 7. The latter figure was drawn from a smaller beetle measuring 6·5 by 3·7 mm., but, despite the disparity in size between the two beetles, the greater size of the coxa in the usual form is striking and also the greater length of the internal lamina of the coxa. It was noticed that the elytral epipleur (fig. 8, *EE*) was slightly wider in the region of the episternum in both specimens with the broad " wings " and that it then tapered more abruptly than in the normal form.

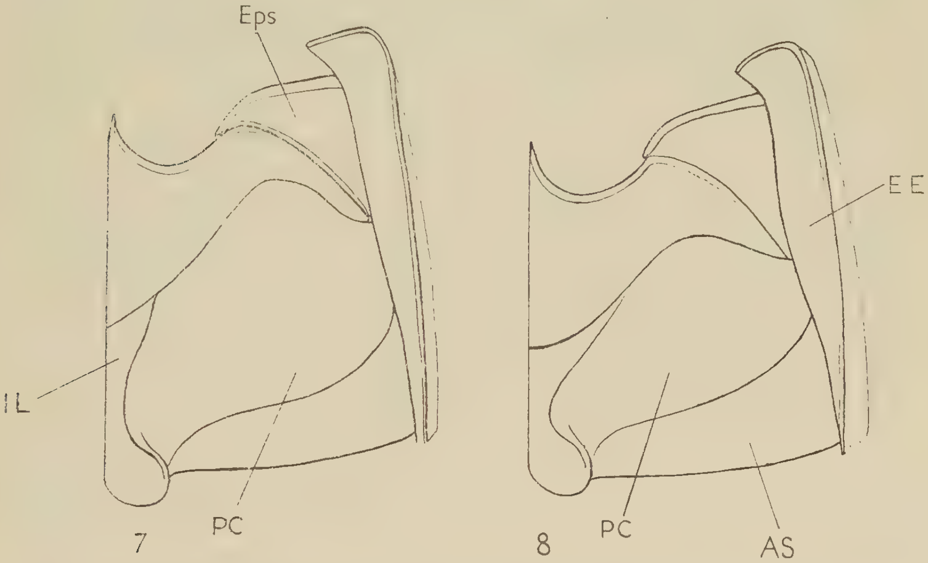


Fig. 7–8.—*Agabus labiatus* Brahm. (7) External view of left half of metasternum and post-coxa with met-episternum and base of elytron, showing the narrow metasternal wing typical of this species. From a female measuring 6·5 by 3·7 mm., with abnormal flight muscles, collected Woolmer Pond, Hants, 12.iv.54. × 21·7. (8) The same but from a female from Sweden measuring 7 by 4 mm., with wide metasternal wings ; without normal flight muscles. Collected Skåne, v.1880 (*C. Roth*). × 21·7.

The anterior coxal fold in the usual form of *labiatus* is as prominent as in the the flightless form of *A. raffrayi*, and may be seen projecting anteriorly well beyond the metasternal wing when the met-episternum is removed, but in the specimen with broad metasternal wing this apodeme does not reach the edge of the " wing ", though it is larger than in the specimens of *raffrayi* with normal flight muscles.

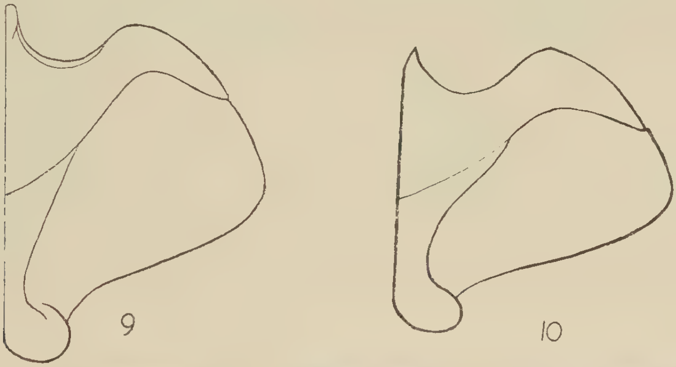
The metatergum and the pleural discs of the specimen of *labiatus* with wide metasternal wings were just like the usual form and no normal flight muscles were present, though the tubular muscles were distinct. There was much fat body in the metathorax and what appeared to be one abnormal flight muscle was seen. The flexor trochanter muscles, in conformity with the smaller hind coxa, were shorter than in the common form. The membranous wings were larger, measuring 7·5 mm., while the elytron measures 5·36 mm. The largest wing of the usual form I have seen measured 6·83 mm. and the elytron 5·15 mm. and the smallest wing 5·83 mm. (elytron not mounted), both these specimens from Fife.

DISCUSSION.

The facts now recorded prove that the shape of the metasternal wings is not a reliable taxonomic character. Sharp (1882) considered this character unsuitable for a natural classification owing to its variability and to the fact that species exhibiting it were not allied by other characters, and Prof. F. Balfour-Browne (1938, 1950) considers this character useless as a group separator. I have already suggested, in a paper now in press (Jackson, 1956), that narrow metasternal wings in *Agabus* and *Platambus* may be correlated with loss of flight; their occurrence in the flightless form of *A. raffrayi*, while broad metasternal wings occur in the form with a fully developed flying apparatus, gives support to this view. It is of great interest to find in this species two distinct forms occurring which exhibit all the characters that I have hitherto found only in flying and in flightless species. In many Dytiscidae I have found variation within a species in regard to the degree of development of the flight muscles and their supports (Jackson, 1952), but this variability has not been combined with a marked difference in the size of the flying wings (except in our smaller *Noterus*), or with variation in the metasternum. In the flightless form of *A. raffrayi* the narrow metasternal wings, the large anterior coxal fold, the reduced metatergum and pleural discs, the absence of normal flight muscles and a more or less pronounced shortening of the wings, are all characters which I have found in *A. undulatus* Schr., *A. labiatus* and *Platambus maculatus* L., and they are fully discussed in the paper in press. The form of *A. raffrayi* with wide metasternal wings presents all the characters found in such good fliers as *Agabus bipustulatus* L., *A. chalconatus* Panzer and others, and I have no doubt that this form of *raffrayi* will disperse readily by flight.

In my experience, wide metasternal wings are present in all good flying *Agabus*, but they are not always accompanied by normal flight muscles, for in *A. guttatus* Paykull, in which the " wings " are wide, I have not found the flight muscles fully developed in any specimen. Comparable to *guttatus* is the form of *A. labiatus* with wide metasternal wings, since the one specimen dissected is also without normal flight muscles, and I believe it to represent a more primitive form of the species.

It seems to me most likely that an arrest in the development of the flight muscles and their supports has been the first step in the degeneration of the flying apparatus, and that this has been followed in some species by narrowing of the metasternal wings and sometimes also by a reduction in size of the flying wings. It is interesting to find that in *Agabus bifarius* Kirby, in which the flying wings may be reduced to narrow slips (Leech, 1942), the metasternal wings are narrow in the three brachypterous specimens I have examined (fig. 9), and the metatergum and pleural discs are even more reduced than in the flightless *A. raffrayi*. *A. maderensis* Wollaston is another species known to have reduced wings, though Professor Balfour-Browne also records finding specimens with fully developed wings (1950). I have examined the wings of fifteen specimens, all but two most generously given to me by Mr. R. C. Fisher. In all, the wings are reduced, but they vary in size from 4·1 to 5·0 mm. and the apical region of the wing varies in outline and in distinctness of venation. The metatergum and the pleural discs are rather more reduced than in *A. bifarius* and the metasternal wings, which vary a little in shape, are fairly narrow, except towards the apex (fig. 10). The post-coxa is short in all the specimens. Dissection shows that the anterior coxal fold is not strongly developed and the furca is smaller than I have seen in any *Agabus*. Unfortunately in none of the specimens dissected were the extensor trochanter muscles (which arise from the furca) well preserved, but, from the anatomical details mentioned, I would surmise that this species is below the average in the development of the muscles of the hind legs. According to Wollaston (1854) *A. maderensis* is abundant in mountain torrents, and Mr. Fisher took it in July 1954 in very small pools and in shallow rills in a wet ravine, conditions which would not allow scope for much swimming.



FIGS. 9–10.—(9) *A. bifarius* Kirby. External view of left half of metasternum and post-coxa, from a whole specimen. From Hudson Bay. × 21·8. (10) *A. maderensis* Wollaston. External view of left half of metasternum and post-coxa, from a whole specimen. From Madeira. × 21·8.

Narrow metasternal wings in *Agabus* are, however, usually correlated with a corresponding enlargement of the hind coxa and an increase in development of the flexor muscles of the hind leg. Narrow metasternal wings are not always correlated with reduced flying wings, since in *A. labiatus* the membranous wings show as a rule very little reduction, whereas in *bifarius* they are greatly reduced. An even more striking instance of this is shown in *Agabetes acuductus* Harris, sent me from Michigan by Dr. F. N. Young. This species has narrow metasternal wings and large hind coxae and the extensor trochanter muscles are so greatly developed as to fill up the metathorax ; the flight muscles are undeveloped and the metatergum is reduced, yet the wings which must be useless for flight are of full size, in one specimen measuring 7·4 mm. while the elytron is 5·4 mm.

In conclusion it is evident that flight reduction has followed different lines in different species and in different groups, and it is sometimes associated with a great development of the muscles of the hind leg. While, in the genus *Agabus*, the species I have so far examined with narrow metasternal wings are flightless, in some other genera narrow metasternal wings are combined with excellent powers of flight (Jackson, 1956). Since two large flight muscles arise from the metasternum, the important factors will doubtless be the total size of the metasternum and the precise arrangement of the muscles in each natural group of species. A reduction of the side pieces of the metasternum is noted by Sir Guy Marshall (1944) as one of the characters correlated with loss of the power of flight in Curculionidae, and Rüschkamp (1927) has found that, in the genus *Chrysomela*, there is shortening of the metasternum according to the degree of wing reduction.

SUMMARY.

Dimorphism has been observed in the metasternal wings of *Agabus raffrayi* Sharp and *A. labiatus* Brahm, which shows that the shape of the metasternal wings is not a reliable taxonomic character.

The specimens of *raffrayi* with wide metasternal wings had a well-developed flying apparatus, but those with narrow metasternal wings were flightless.

The form with narrow metasternal wings has been named *pallidus* Omer-Cooper, but the evidence here brought forward shows that it is merely a flightless form of *raffrayi*.

In *A. labiatus* the normal form has narrow metasternal wings and all the specimens dissected have been flightless. Two Swedish specimens were found to have wide metasternal wings, and one of these was dissected and was without normal flight muscles.

The evidence so far available suggests that in the genera *Agabus* and *Platambus* narrow metasternal wings are correlated with loss of flight.

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EXPLANATION OF LETTERING.

ACF, anterior coxal fold.
ANP, anterior notal wing process.
AP, apical plate of postnotum.
AS, abdominal sternite, apparent first (true second).
BaMD, basalar muscle disc.
CL, coxal line.
CP, coxal process.
EE, elytral epipleur.
EAA, extensor alae anterior.
EAP, extensor alae posterior.
Eps, episternum of metathorax (metepisternum).
IL, internal lamina of coxa.
M, metasternum.
MDP, muscle disc on prescutum of *musculus relaxator alae.*
MW, metasternal wing.
PC, post-coxa.
PN, postnotum.
PPh, postphragma.
Sa, subalar disc.
Sp, spiracle of first abdominal segment.

SOME FURTHER OBSERVATIONS ON THE NATURE OF "QUEEN SUBSTANCE" AND OF ITS ROLE IN THE ORGANISATION OF A HONEY-BEE (*APIS MELLIFERA*) COMMUNITY.

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Introduction.

Müssbichler (1952) and others have shown that provided young bees are fed on a diet containing carbohydrate and sufficient protein, or on a pure carbohydrate diet after they have eaten sufficient protein, their ovaries develop when no queen is present. Ovary development does not appear to be possible unless protein is available to the bees concerned either in their diet or as reserves within their own bodies.

Although the ovaries of workers do sometimes develop to a limited extent when a queen is present (Perepelova, 1929 ; Maurizio, 1954) experiments have shown that no queen must be present if the ovaries of any workers are to develop quickly and to any considerable extent (Peterka, 1929 ; Hess, 1942 ; Pain, 1954 ; de Groot and Voogd, 1954). It appears probable, therefore, as suggested by Butler (1954) and Pain (1954), that worker honey-bees normally obtain an ovary-inhibiting substance from the bodies of their queens. Indeed de Groot and Voogd (1954) have succeeded in obtaining potent extracts of such a "queen substance" both in ethyl alcohol and in acetone. Similar extracts of queen substance in organic solvents were also prepared by the author during the summer of 1954. (*Unpublished work.*)

Present data suggest that the worker bees of a colony normally make no attempts to rear queens provided that they regularly receive adequate supplies of some substance from their queen (Butler, 1954). These data also indicate that this "queen substance" is present on all parts of the body surface of a queen from whence the workers obtain it.

If it is the same substance which inhibits both the development of the ovaries of worker honey-bees and the urge of the latter to rear queens, one would expect development of the ovaries of the workers whenever the amount of queen substance available to the members of a colony falls below a certain threshold and queen cells are built. Indeed Perepelova (1929) found developing ovaries in some workers of colonies in which new queens were being reared preparatory to swarming.

Thus the queen substance theory appears to explain the two phenomena of queen production and of worker ovary development. However, the problem remains of the method by which the queen substance becomes distributed amongst the members of a large colony. It seems impossible that every worker should receive a supply *directly* from her queen, as de Groot and Voogd (1954) have suggested, because each worker needs to receive a supply every few hours to remain inhibited from queen production (Butler 1954). Furthermore, regular introduction of sufficient workers who have just been with a queen to other queenless and well nourished workers is sufficient to suppress queen cell production by honey-bees (Butler, 1954) and ovary development in ants (Bier, 1954).

Experiments were made, therefore, to determine whether or not the queen substance obtained by worker bees licking their queen is then subsequently passed from bee to bee in regurgitated food, as suggested by the results of earlier observations (Butler, 1954).

EXPERIMENT I.

One hundred newly-emerged worker honey-bees of an Italian strain were taken at random, and 50 were placed in each of two cages (A and B) in an incubator at approximately 31° C. Each cage (6·3 cm. wide × 9·5 cm. high × 4·3 cm. deep) was made largely of wire-gauze and contained a small piece of comb upon which the bees tended to cluster. Abundant supplies of honey (slightly diluted with water), fresh bee-collected pollen, and distilled water were continuously available in each cage.

Every day six worker bees were caught just after licking a mated, laying queen honey-bee and were introduced to the bees in cage A directly after bees added on the previous day had been removed. No additional bees were introduced into cage B which served as a control.

After 13 days 40 of the bees in each cage were dissected. It was found that every bee contained a large amount of pollen and that her fat-body had developed to some extent. The degree of development of the ovaries of each bee was determined, and classified as follows : (*a*) Undeveloped ; (*b*) slightly developed, i.e. some slight swelling of the oviducts and ovarioles ; (*c*) moderately developed, i.e. pronounced swelling of the oviducts and ovarioles and clear evidence of egg formation ; (*d*) well-developed, i.e. as in *c* but ovarioles clearly full of eggs in all stages of development. The results obtained are shown in Table I.

TABLE I.—*The effect on the ovary development of a group of queenless worker bees of regularly adding worker bees caught licking a queen to their group.*

	Ovary development.			
	Well developed.	Moderately developed.	Slightly developed.	Undeveloped.
Experimental bees (Cage A) .	3	8	11	18
Control bees (Cage B) . .	18	15	6	1

The difference in the degree of development of the ovaries of the bees forming the two groups is highly significant ($P < 0{\cdot}001$). This suggests that the addition of the workers who had been licking a queen to the experimental group of bees was sufficient to retard the development of their ovaries. This could be explained by supposing that the bees which were added to the queenless group shared the queen substance they had just licked off a queen with the bees of this group.

To obtain further evidence the following experiments were carried out.

EXPERIMENTS II AND III.

One hundred and twenty newly emerged worker honey-bees were divided equally between two cages, C and D, similar to those used in the previous experiment, and were kept at about 31° C. A plentiful supply of dilute honey and of fresh bee-collected pollen was maintained in each cage.

Six worker bees were caught each day whilst they were licking a mated, laying queen and their entire honey-stomachs, oesophagi and mouthparts were macerated in 1 c.c. of distilled water and filtered. The resulting fluid was made freely available to the experimental bees in cage C. A fluid similarly prepared from bees who had been kept away from any queen for three days was fed to the control bees in cage D.

After 10 days 50 bees in each cage were dissected. The alimentary canal of every bee contained much pollen and their fat-bodies had developed. The degree of development of the ovaries of each bee was determined, the same four categories of development being adopted as in the previous experiment.

This experiment was repeated, and the results of both experiments are given in Table II.

TABLE II.—*The effect of feeding the honey-stomach contents of bees caught licking a queen on the ovary development of queenless workers.*

	Ovary development.			
	Well developed.	Moderately developed.	Slightly developed.	Undeveloped.
Experiment II :				
Experimental bees .	1	3	27	19
Control bees . .	23	20	7	0
Experiment III :				
Experimental bees .	0	9	19	22
Control bees . .	27	16	6	1

The differences between the degrees of development of the ovaries of the experimental and control bees in these two experiments are highly significant ($P < 0{\cdot}001$).

DISCUSSION.

The data obtained in Experiment I suggest that bees who have just licked the body of a mated laying queen can, temporarily, take the place of a queen to some extent and retard development of the ovaries of a number of workers with whom they come into contact. The further data obtained in Experiments II and III suggest that the fore-gut of a bee which had just licked a mated, laying queen contains some substance which has a repressive effect upon the development of the ovaries of workers to whom it is fed.

It seems reasonable to conclude, therefore, that the substance which worker bees obtain from the body surface of a queen is shared in regurgitated food with other bees. This substance, if sufficiently abundant, causes suppression both of ovary development in the bees concerned and of their urge to rear queens.

All the evidence at present available [e.g. Hess (1942) ; Müssbichler (1952) ; Butler (1954) ; Pain (1954) ; de Groot and Voogd (1954)—honey-bees ; Bier (1954)—ants] suggests that worker ants and honey-bees (also probably termites) must have physical contact at regular intervals either directly with their queens or with other workers who have very recently done so to have their ovary development inhibited, and that some substance (queen substance) passes between the individuals concerned. This last point has not been recognised by all investigators. Conflicting conclusions have arisen because it has not been realised that little food exchange, and therefore little queen-substance sharing, takes place between the members of well-fed groups of honey-bees that are separated from each other by a wire-gauze screen (Free and Butler, 1955).

The ovaries of all the members of a well-nourished group of queenless honey-bees, of the same age and belonging to a single colony, do not develop to the same extent in a given period of time (Experiments I, II and III). This suggests that something is produced by those bees whose ovaries develop first which inhibits ovary development in the other bees.

As mentioned by Wigglesworth (1954), it is not yet known whether the queen substance acts directly upon the metabolism of a worker, or whether it merely serves as a " trigger " mechanism resulting in the release within the body of a recipient bee of a hormone which is the actual inhibitor both of ovary development and of the urge to rear a new queen. If it is only a releasing mechanism there is, of course, a likelihood that still other releasing mechanisms exist, possibly psychological ones.

SUMMARY.

(1). It is known that worker honey-bees obtain some substance from their queens which results in inhibition of development of their ovaries. It is also known that some substance obtained from the queen of a colony, if sufficiently plentiful, inhibits queen production. It is concluded that a single " queen substance " serves both these functions.

(2). It has been suggested that queen substance is obtained by some members of a colony licking their queen, and that they share it in regurgitated food with other members of their colony. It is now demonstrated that this does in fact occur.

(3). It is not yet known whether the queen substance acts directly on the metabolism of the bees who receive it, or whether it merely acts as a trigger mechanism and releases a hormone which inhibits ovary development. If queen substance only acts as a trigger mechanism it is quite likely that still other releasing mechanisms exist.

ACKNOWLEDGMENTS.

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X-RAY INDUCED MUTATIONS IN MOSQUITOES.

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Kitzmiller (1953), in an excellent review entitled *Mosquito Genetics and Cytogenetics,* has stressed the need for more genetical studies of all kinds on mosquitoes, emphasising particularly the " need for . . . morphological genes . . . as markers and testers " not only with a view to building up a formal genetics of mosquitoes comparable with that available for *Drosophila* and other experimental animals employed in this field, but as an aid to the solution of various grave problems in medical entomology.

It is here proposed to mention only two problems of this nature which seem clearly to demand a genetical approach. After World War II there arose in many parts of the world the question as to whether indigenous mosquitoes would be capable of infection with exotic strains of malaria brought back by returning troops and of transmitting such strains to the human population. As Huff (1927, 1929, 1931) demonstrated some time ago, susceptibility to infection with malaria parasites behaves, at least in *Culex pipiens*, as a Mendelian character. Whether this is also true of other mosquitoes or of infection with exotic strains is still unknown.

Another serious problem at the present time is the increasing number of insecticide-resistant strains of mosquitoes reported from various parts of the world. Many studies of insecticide resistance and susceptibility in *Drosophila* have revealed that these are genetical traits. As yet no such approach is possible in mosquitoes by reason of our lack of fundamental knowledge regarding their genetics and, in particular, of marker genes.

My own interest in mosquito genetics has a different origin. In the course of several years' work on the biology and systematics of the *Culex pipiens* complex I encountered a curious type of reproductive incompatibility as between various European and American populations of the species concerned (Laven, 1951, 1953 ; Laven and Kitzmiller, 1954). Some populations can be crossed in both directions with complete success. Others are completely isolated by intersterility in both directions and yet others can be crossed in one direction only. I have tried to explain this non-reciprocal compatibility as a case of cytoplasmic inheritance. In order to secure full confirmation of this hypothesis I found it necessary to isolate mutant genes from among the experimental populations. A search for spontaneous mutations met with only partial success. Only two colour differences in the fourth stage larvae and a hereditary form of intersexuality have as yet been found. However, a single treatment of two-to three-day-old males of *Culex pipiens* with X-rays (4000r) has already produced several very promising visible aberrations which have proved to be heritable. Using these mutants it will be possible to mark each of the chromosomes in the *Culex* nucleus with at least one gene, and probably with more, since in this genus the haploid number of chromosomes is only three. It will thus be possible to lay the foundations of a formal genetics in *Culex* by marking chromosomes and working out the first linkage groups. Work on these lines has already started in our laboratory. Two of the mutations appear to mark the autosomal chromosomes because they are independent of sex. A third is clearly sex-linked and a fourth behaves similarly, but is not a good marker because it is coupled with a lethal factor or factors. These first-noted mutations produce gross aberrations in morphology, but it may be expected that by the use of more refined methods it will later be possible to detect smaller differences which are genetical in nature. Three of the as yet found mutations are aberrations of wing venation. The others affect the male and female palps and antennae. A brief description is given here for the benefit of those interested in mosquito biology. The mutant strains will be maintained in our laboratory for further research and they will be available to other workers on request.

(1) *Rap* (figs. 1–4) is a dominant autosomal affecting palps and antennae of both sexes. Normally the antennae have 13 segments. Animals with the mutant *Rap* have the antennae reduced to about half the normal length. At the same time the male palps are shortened and the terminal joint is lost.

(2) *kps* (fig. 5) is a recessive autosomal. In this case the terminal segments of the male palp are transformed into a sort of hinged claw which is developed symmetrically on both palps.

(3) *Kpu* (fig. 6) is a dominant sex-linked factor. Unlike the factor *kps*, this factor is expressed, in most cases, very asymmetrically. It affects the terminal segment of the male palps and appears in this sex only.

(4) *var* (figs. 7–8) is recessive and sex-linked. Veins r_3 and r_{4+5} join at the wing-tip to form a common stalk. This is confined to the female sex as long as no cross-over occurs.

These four mutations seem to mark all the existing chromosomes in *Culex*, the two autosomes and the sex chromosomes of each sex. Certain other mutations have been encountered, but their mode of inheritance has not yet been fully elucidated. Two of them are clearly defined mutations affecting wing venation. Information regarding the genetics of these mutations will be published later.

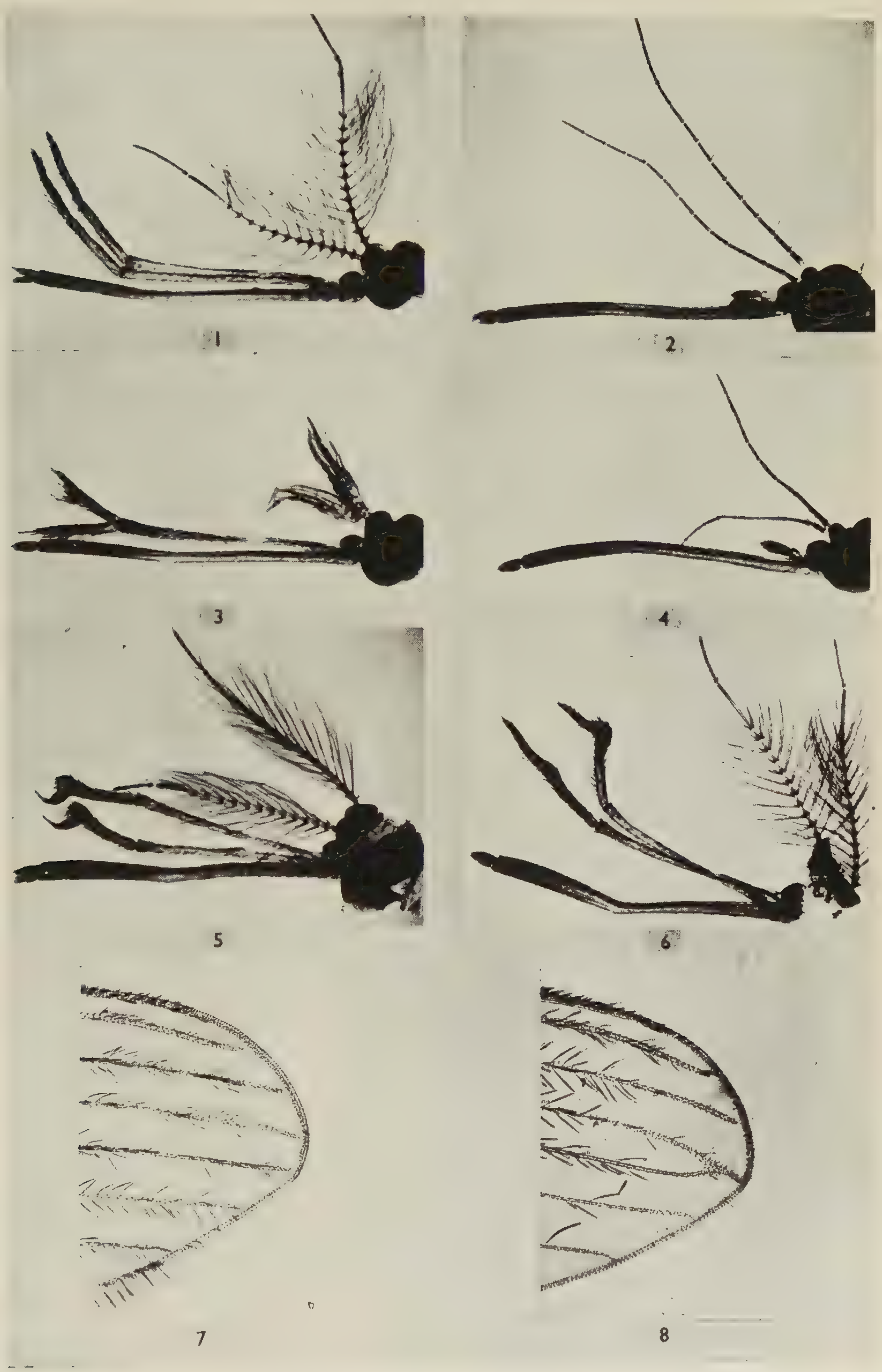
SUMMARY.

The urgent need for a genetical approach to certain problems in the field of mosquito studies has made it necessary to produce mutations in these animals by treatment with X-rays. Certain of the mutations obtained in this way in *Culex pipiens* are here described. They promise to be of considerable value for the study both of formal genetics and of applied biology.

PLATE I.

Culex pipiens

1. Head of normal male.
2. Head of normal female.
3. Head of male with mutation *Rap*.
4. Head of female with mutation *Rap*.
5. Head of male with mutation *kps*.
6. Head of male with mutation *Kpu*.
7. Normal venation at wing tip.
8. Venation at wing tip with mutation *var*.



X-ray induced mutations in mosquitoes.

H. Laven.

Adlard & Son, Ltd., Dorking.

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THE *GEORYSSUS* LARVA-A HYDROPHILID.

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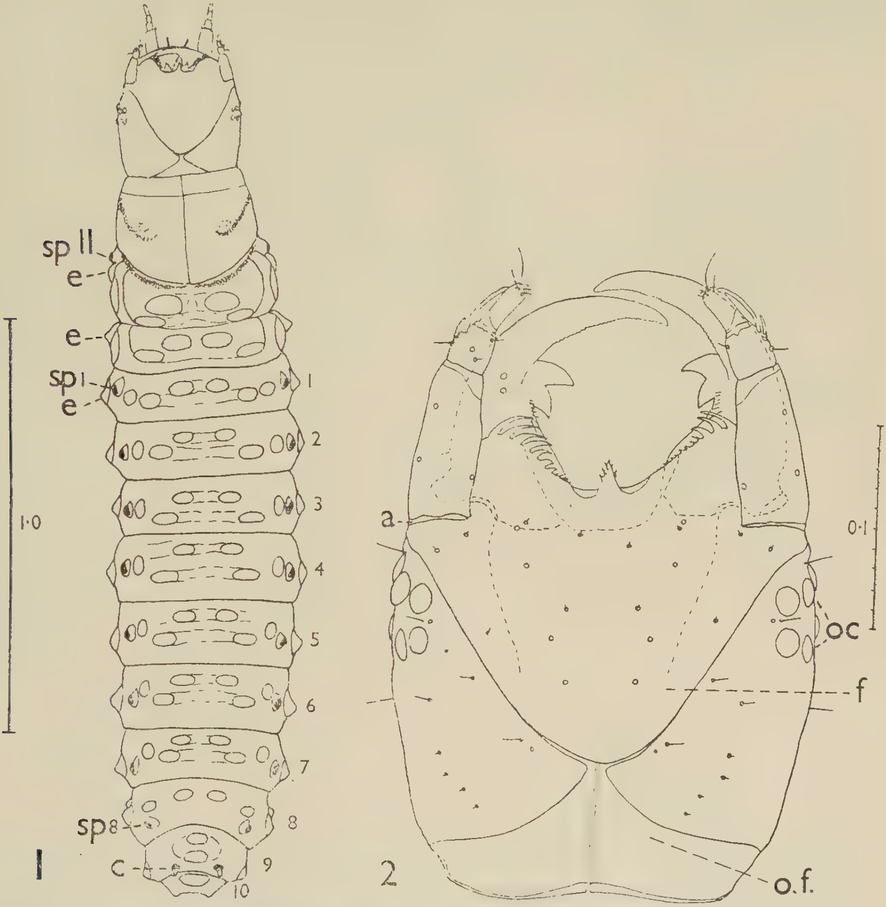
Among the few groups of British beetles which have been given family rank and of which the larva has remained unknown the Georyssidae are one of the most interesting, as various authors have placed them in different groups of Coleoptera. Thus Erichson and Ganglbauer placed them between Byrrhidae and Dryopidae, Kolbe near Hydrophilidae (together with the Lathridiidae, Thorictidae, Elmidae, etc.) and not very closely to Byrrhidae and Dryopidae. Sharp and Muir believed in some relationship with the Gyrinidae and Hydrophilidae. Meixner placed them in " Dryopida " but mentioned Sharp and Muir's view as an alternative. Crowson recently, from a study of the adult, considered relationship with the Hydrophilidae as very probable.

From a correspondence with Herr Heinrich E. Wichmann of Hebertshausen, near Munich, I learned that at a place easily accessible to him *Georyssus crenulatus* Rossi was common, as sampling led him to estimate the population at various times at 30, more than 80 and more than 220 specimens per square meter. Herr Wichmann was kind enough to study for me an area of 9 × 9 cm. up to a depth of 1 cm. under a binocular microscope, and he found, in addition to larvae, pupa and adult of *Syncalypta paleata* Er. (the larva much like *Byrrhus* but with a concave dish-like ninth tergite somewhat similar to that of *Phaleria* and *Meracantha*) and a larva related to *Oxytelus*, two small larvae which clearly seemed to belong to the Hydrophilidae, being reminiscent of Sphaeridiinae.

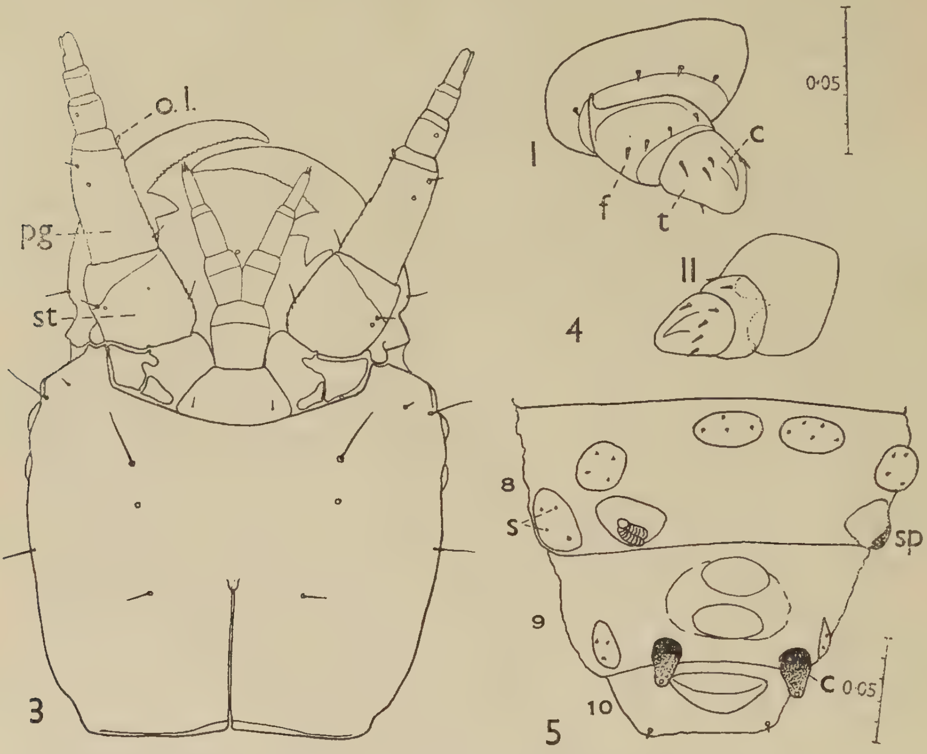
These two larvae moved sluggishly on the surface of the clay soil, which was covered with slimy algae and sparse mossplants. A closer study revealed that they clearly are Hydrophilidae though not belonging to any known subfamily. The subfamilies of Hydrophilidae fall into two groups, the first, more primitive, group with ten free abdominal segments, 1 + 8 pairs of spiracles, all situated on the dorso-lateral part of the segments, distinct free cerci on the ninth tergite, and the antennal foramen reaching farther laterad than the point of articulation of the mandible. Of the known subfamilies, Hydraeninae, Limnebiinae and Helophorinae are united in this group. In the second group only eight normal abdominal segments (in Spercheinae " apparently " nine) are present; the spiracles of the eighth abdominal segment are large and enclosed in a breathing atrium formed by the eighth segment and the vestigial ninth (and presumably tenth), so that the minute cerci are found in the atrium (all this applies to *Spercheus*, although the atrium there is smaller and has sometimes been overlooked). The other spiracles are absent, vestigial or at any rate much smaller. Spercheinae and Hydrochinae on the one hand, with the antennal foramen as in the first group, and Sphaeridiinae and Hydrophilinae on the other, with the antennal foramen not extending laterad to the dorsal articulation of the mandible, form this second group of subfamilies.

The larvae from Hebertshausen have ten free abdominal segments (fig. 1, *1–10*), 1 + 8 free dorso-lateral spiracles (fig. 1, *sp.II*, *sp.1*, *sp.8*), free cerci (figs. 1 and 5,*c*) and widely separated antennal foramina (fig. 2,*a*). In spite of their Sphaeridiine legs (fig. 4) they are thus related to Hydraeninae, Limnebiinae and Helophorinae. As in the latter subfamily and differently from Hydraeninae and Limnebiinae the frontale (fig. 2, *f*) reaches the occipital foramen (*o.f.*), six ocelli are present (fig. 2, *oc*), the mandible has no prostheca and mola but a large retinaculum, the maxilla has no inner lobe and no outer lobe on stipes (fig. 3, *st*), but a small outer lobe (fig. 3, *o.l.*) on palpiger (*pg*), the ligula is entirely absent, the ventral mouthparts are only slightly retracted, the spiracles bicameral (fig. 5, *sp*), and the tenth abdominal segment (fig. 5, *10*) without a pair of ventral hooks.



FIGS. 1–2.—*Georyssus crenulatus* Rossi. (1) Full-grown larva, dorsal view. *1*, *2*, etc., abdominal segments 1, 2, etc.; *c*, cercus; *e*, epipleurite; *sp II*, spiracle of mesothorax; *sp 1*, *sp 8*, spiracles of first and eighth abdominal segments. (2) Half-grown larva, head, dorsal view. *a*, antennal foramen; *f*, frontale; *oc*, ocelli; *o.f.*, occipital foramen.

The Hydrophilid larvae found at the *Georyssus* locality thus are most closely related to the Helophorinae, but this subfamily has long three-segmented cerci (whereas the new larva has short one-segmented ones), long, fully segmented legs (whereas the larva here described has very short stumpy legs with reduced segmentation), a normal short appendage at the second antennal segment (whereas the new form shows an extremely long appendage), a smooth cuticle with large sclerites and outstanding setae (whereas the Hebertshausen larvae have a membranous cuticle with dense wart-like asperities, very small sclerites and minute setae, fig. 5, *s*). These differences are so striking and important that the larvae found at the *Georyssus* locality will have to form a new subfamily of Hydrophilidae following closely after the Helophorinae.



FIGS. 3–5.—*Georyssus crenulatus* Rossi. (3) Half-grown larva, head, ventral view. *o.l.*, outer lobe of maxilla; *pg*, palpiger; *st*, stipes. (4) Half-grown larva, legs. *I*, prothoracic leg; *II*, mesothoracic leg; *c*, claw; *f*, fused trochanter and femur; *t*, tibiotarsus. (5) Half-grown larva on slide, last abdominal segments, dorsal view. *8*, *9*, *10*, eighth, ninth and tenth abdominal segments respectively; *c*, cercus; *s*, microscopic setae; *sp*, spiracle of eighth abdominal segment.

Larvae of half the German subgenera of *Helophorus* are known and all very similar, and no other European genus belongs to the subfamily, nor does any other genus occur in Germany the adult of which is placed in Hydrophilidae and the larva of which is unknown, except for *Cryptopleurum*. The latter larva must certainly be expected to have only eight free abdominal segments, a breathing atrium, less widely separated antennal foramina, etc.

In view of the fact that *Georyssus crenulatus* Rossi is common at the locality and that its adult shows many Hydrophiloid features (male genitalia[1], wing folding pattern[2], 9-segmented antennae with a large pedicel and a 3-segmented pubescent club, Y-shaped sutures of the head[3], etc.) there can be little doubt that the larvae from Hebertshausen belong to *Georyssus crenulatus* Rossi, and that the Georyssinae are a new subfamily of the Hydrophilidae, which must be placed between Helophorinae and Spercheinae.

The characters of *Georyssus crenulatus* are illustrated by the figures, and only few supplementary remarks are required.

The two larvae are 1·21 and 2·05 mm. long and their head-widths are 0·20 and 0·29 mm. Head, mouth-parts, pronotum and the small sclerites of the tergites pale testaceous, the rest pale brownish with the asperities darker brownish. Cerci dark brown in basal two-fifths, pale brownish and finely asperate in apical three-fifths. Sclerites strongly convex and therefore conspicuously prominent in lateral view, the spiracular sclerites somewhat less so than the dorsolateral sclerite.

Head moderately flattened, narrowed behind without a defined neck. Second antennal segment bearing on its outer side a very long sensorial appendage and basad of it a small one. The cutting edge of the mandible between the apex and the large double retinaculum is denticulate. Inner surface of the maxillary stipes and long palpiger carry some scale-like asperities. Cardo consisting of two sclerites. No trace of a ligula. Gular suture simple, not quite reaching middle of head-capsule (fig. 3). Pronotal sclerite complete, almost entirely covering dorsum of prothorax. Meso- and metanotum each with two pairs of sclerites, the outer ones at a more posterior level. Mesothoracic spiracle somewhat prominent, bicameral, the slits vertical. Meso- and metathorax with an epipleural sclerite (fig. 1, *e*) below level of the spiracle. Prosternum apparently with three sclerites in a transverse row in front of fore legs. First to seventh abdominal segments each with three pairs of small ovate sclerites, the paramedian ones slightly in front of level of next pair, the dorso-lateral ones longitudinal, level with the spiracular sclerite, the spiracular slits obliquely longitudinal. To its outer side a longitudinal epipleural sclerite (fig. 1, *e*). Ventral surface of typical abdominal segments with four transverse folds. Eighth abdominal segment with only two pairs of sclerites, the outer one and the spiracular sclerite, which lies behind it, rather more projecting, the epipleural sclerite level (in transverse direction) with the spiracular sclerite. Ninth segment (fig. 5, *9*) without paired sclerites but with a pair of widely separated truncate conical cerci, the apex of which carries a small papilla-like structure, presumably the vestigial second segment. Tenth segment (fig. 5, *10*) broad and short, very distinct.

Legs very short and stout, only about a third as long as width of mesothorax, the prothoracic pair (fig. 4, *I*) markedly stouter. Trochanter and femur (*f*) fused, much wider than long, base of claw (*c*) fused with tibiotarsus (*t*), the latter short and stout, ending in a broad membranous convex tip, reminiscent of the adhesive pad of the *Chrysomela* larva.

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Note.—The figures have been made with a camera lucida and (fig. 1) a Baker stereoscopic microscope with eye pieces 10 × and objectives 6 ×, or a Winkel monocular microscope with eye-piece 4 (figs. 2, 3, and 5) or 5 (fig. 4) and a Watson objective 30 ×. The scales are expressed in mm.

LECTOTYPES OF MOSQUITOES (DIPTERA : CULICIDAE) IN THE BRITISH MUSEUM.

Part I. Genera *Aëdes* (Subgenus *Pseudoskusea*), *Armigeres* and *Eretmapodites*.

By P. F. Mattingly, B.Sc., F.R.E.S.

(*British Museum, Natural History.*)

Details have been given elsewhere (Mattingly, 1954) of lectotypes chosen from a collection of material recently presented to the British Museum by the Tropical Institute at Hamburg. During recent years many other lectotypes have been marked from among type series in the collection and it is now desired to validate these by publishing them. Details are given below.

Australian Species.

Genus *AËDES* Meigen. Subgenus *Pseudoskusea* Theobald.

Culex australis Erichson, 1842, *Arch. Naturgesch.* **8** : 270.

The synonymy of this species is discussed elsewhere (Marks & Mattingly *in press*). Through the kindness of Prof. Dr. Fritz Peus it has recently been possible to examine Erichson's type series of one ♂ and two ♀ from the Zoologisches Universitäts Museum in Berlin. Before returning the specimens to Prof. Peus I marked the ♂ as hololectotype, one ♀ as allolectotype and the remaining ♀ as a paratype. Data for all three are " Terr. Van Diem., Schayer ". The ♂ bears the number 5986.

Oriental Species.

Genus *ARMIGERES* Theobald.

Chaetomyia flava Leicester, 1908, *Stud. Inst. Med. Res. F.M.S.* **3** (3) : 101.

The British Museum has three ♀ cotypes of which only one is marked with the locality. This specimen is unfortunately less complete than the others but I have preferred to mark it as the hololectotype since its provenance is known and it is clear from Leicester's account that his type series came from two different types of breeding-place. The data on the back of the mount are " Bamboo, Ulu Klang Jungle 8 miles fr. Kuala Lumpur, 25/9/03." I have marked the two remaining specimens as paratypes.

Desvoidya jugraensis Leicester, *ibid.* : 77.

The British Museum has four cotypes of mixed provenance from Ampang and Jugra respectively. Leicester's description refers to specimens from Ampang, Jugra and Borneo. I have marked a ♂ and a ♀ from Ampang as hololectotype and allolectotype respectively. Both bear the same data on the backs of the mounts. These are as follows: "Larvae from bamboo, Ampang Jungle. Taken 29/1/03. Fly 2/2/03". As paratypes I have marked one ♀ with the data "Larvae, red backed, fr. cut bamboos, Ampang Jungle, 5¾ miles Kuala Lumpur. Larvae 7/2/03. Pupae 9/2/03. Fly 12/2/03", and a ♂ with the data "Leaf, Jugra Jungle, 16/9/04".

Armigeres kuchingensis vars. *dibrugharensis*, *nongpohensis* and *shillongensis* Barraud, 1927, *Indian J. med. Res.* **14**: 539.

Barraud did not mark types of any of these varieties. The taxonomic value of the names is very dubious since numerous intermediates are stated by Barraud to occur. The British Museum has only four specimens from Assam and since none of these conforms precisely to any of Barraud's descriptions I have preferred not to choose lectotypes. Better material is probably to be found in the collection of the Malaria Survey of India.

ETHIOPIAN SPECIES.

Owing to his untimely death the late Dr. Edwards was unable to mark types of most of the new species described by him in Volume III of *Mosquitoes of the Ethiopian Region* (Edwards, 1941). It has, however, been possible in all cases to identify and separate his type series. In some cases the data quoted by him in his citation of the type are applicable to only one specimen. Where this is so I have marked the specimen as the holotype. In other cases I have chosen and marked lectotypes. Edwards also failed to mark types of certain species described by Graham and Theobald although he indicates in his book that he has done so. In these cases also I have marked lectotypes from among the type series. Details of some of these follow. Genera not included here are dealt with in a second paper at present in the press.

Genus ERETMAPODITES Theobald.

Eretmapodites silvestris ssp. *conchobius* Edwards, 1941, *Mosq. eth. Reg.* **3**: 231.

Described from 1 ♂ and 2 ♀, KENYA: Tiwi, vii.1939; 3 ♂, KENYA: Shimba Hills, vii.1939; and 1 ♂, KENYA: Malindi, viii.1938 (all coll. *E. C. C. Macdonald*). The British Museum has the whole series except for 2 of the ♂ from Shimba Hills. Edwards cites the ♂ from Tiwi as type and I have marked this as the holotype and the other specimens as paratypes.

Eretmapodites penicillatus Edwards, *ibid.*: 234.

Described from 1 ♂, NIGERIA: Ilesha, 8.x.1910 (*L. E. H. Humfrey*); and 1 ♀, SIERRA LEONE: Freetown, xii.1904 (*F. Smith*). Edwards cites the ♂ as type and I have marked this as holotype and the ♀ as a paratype.

Eretmapodites oedipodius ssp. *stanleyi* Edwards, *ibid.*: 239.

Described from 3 ♂ and 3 ♀, ix.1929 (*J. Schwetz*); 2 ♂, viii.1929 (*J. Schwetz*); 1 ♂ and 3 ♀, x–xi.1929 (*J. Schwetz*); 1 ♀, v–vii.1928 (*J. Schwetz*); 4 ♂ and 6 ♀, undated (*Mouchet*); 4 pupal pelts, iv.1928 (*J. Schwetz*); and 2 pupal pelts, undated (*J. Schwetz*); all from Belgian Congo: Stanleyville. I have marked a ♂ collected by Schwetz in ix.1929 as hololectotype and the other specimens as paratypes. The British Museum also has a slide of whole larvae from Stanleyville, coll. J. Schwetz, undated, but, as there is no evidence that Edwards took these into account in drawing up his description, I have left them unmarked.

Eretmapodites oedipodius ssp. *parvipluma* Edwards, *ibid.*: 240.

Described from 1 ♂ and 3 pupal pelts, Uganda: Kasuku, 24.iv.1931 (*G. L. R. Hancock*); 1 ♀, Uganda: Damba I., Lake Victoria, 30.vii.1911 (*G. D. H. Carpenter*); and 1 ♀, Belgian Congo: Bobendana, ix.1939 (*J. Schwetz*). Edwards (1941) clearly indicated that the ♂ was to be the holotype and I have marked it as such. He appears to have wished to exclude from the type series the ♀ adult from the Shimba Hills, Kenya, vii.1939 (*E. C. C. Macdonald*), and accordingly I have left this unmarked.

Eretmapodites oedipodius ssp. *wansoni* Edwards, *ibid.*: 240.

Described from 2 ♂, Belgian Congo: Matadi, 25.v.1938 (*M. Wanson*). The British Museum also has some whole larvae and pupae with identical data but as these were not referred to by Edwards I have left them unmarked. I have marked one ♂ adult as the hololectotype and the other as a paratype.

Eretmapodites leucopus ssp. *productus* Edwards, *ibid.*: 241.

Described from one ♂, Belgian Congo: Stanleyville, vi.1928 (*J. Schwetz*); 6 ♂ and 2 ♀, Belgian Congo: Nzebi, near Mongbwalu, x–xi.1939 (*J. Schwetz*); and a pupal skin from Stanleyville, vii.1928 (*J. Schwetz*). Edwards specifically designated the ♂ from Stanleyville as holotype and I have marked it as such. I have marked the other specimens as paratypes. The British Museum also has a ♀ from Belgian Congo: Kalukulu Lundu, 22.ix.1937 (*Mortiaux*). Edwards mentioned this specimen but appears to wish to exclude it from the type series. Accordingly I have left it unmarked.

Eretmapodites plioleucus Edwards, *ibid.*: 241.

It has not been necessary to mark the holotype ♂ since Edwards himself did this. The species was described from one ♂ and one ♀, the former being chosen as the holotype. Some confusion exists as to the type locality. This is, in fact, Gold Coast: Kumasi, 23.x.1907 (*W. M. Graham*). In one part of his description Edwards indicates that it is Kumasi and in another that it is Obuasi, Gold Coast. The latter is the locality for the ♀ which I have marked as a paratype, 13.xi.1907 (*W. M. Graham*).

Eretmapodites plioleucus ssp. *brevis* Edwards, *ibid.*: 242.

Described from one ♂ and one ♀, Belgian Congo: Stanleyville, undated (*Mouchet*). Edwards designated the ♂ as holotype and I have marked it as such. I have marked the ♀ as a paratype.

Eretmapodites oedipodius Graham, 1909, *Entomologist* **42** : 86.

The British Museum has 3 ♂ and 3 ♀ from Gold Coast : Obuasi, various dates in October and November 1907 (*W. M. Graham*). These are presumed to have formed part of Graham's type series. I have marked a ♂, dated 5.xi.1907, as hololectotype and the remaining specimens as paratypes.

Eretmapodites leucopus Graham, *ibid.* : 88.

Described from specimens from Gold Coast : Obuasi and Kumasi. The British Museum has 2 ♂ from Obuasi, 8.xi.1907 (*W. M. Graham*). I have marked one of these as the hololectotype and the other as a paratype.

Eretmapodites melanopus Graham, *ibid.* : 158.

Described from specimens from Gold Coast : Obuasi. Edwards (1911) notes that the series sent to the British Museum by Graham included specimens of *E. chrysogaster* Graham and a species resembling *E. inornatus* Newstead (1907). Edwards (1941) proposed to mark as lectotype one of the two specimens resembling *E. inornatus* which were available to him. He did not do this although he segregated the two specimens under the name *melanopus* and placed the remainder of the series under *E. chrysogaster*. It has not been possible to identify the specimens placed under *E. chrysogaster* except for one which is dated 21.vi.1907 and so must have belonged to Graham's *E. melanopus* series since this was the only one of the four species described by him which he took in the month in question. In addition this specimen has an exceptionally dark mesonotum (it closely resembles the dark variety of *E. chrysogaster* described by Edwards (1941 : 227).) In this respect it agrees particularly well with Graham's description of *E. melanopus* and, had I felt free to do so, I should unhesitatingly have chosen it as the lectotype. It appears to me, however, that Graham's description of the mesonotum is too generalized to exclude the specimens chosen by Edwards and since it seems certain that the former had these before him when making his description I have followed Edwards and marked one of them as hololectotype. The specimen in question is dated 21.vii.1907 and the other, which I have marked as a paratype, is dated 11.viii.1907. I have also marked the specimen collected in June as a paratype and have segregated this, together with the specimens from Uganda and Belgian Congo described by Edwards, under the name *E. chrysogaster* var. I have left unmarked a similar specimen, dated 22.vi.1906, which I found in the duplicate collection. This was presented to the Museum on a separate occasion and presumably did not form part of Graham's type series.

Eretmapodites chrysogaster Graham, *ibid.* : 157.

Described from a mixed series of specimens including some of a species included by Theobald (1901) in his description of *E. quinquevittatus* and others later described by Edwards (1914) under the name *E. chrysogaster* var. *semisimplicipes*. Edwards (1914) chose to attach the name *chrysogaster* to the first of these two species and marked a lectotype accordingly. Data for this specimen are Gold Coast : Obuasi, 13.xi.1907 (*W. M. Graham*). Later Edwards (1941 : 228) found that Graham (*in* Theobald 1910) had figured the terminalia of the second species as those of *E. chrysogaster*. In my view this finding does not, as Edwards feared, invalidate his choice of lectotype since the drawing was published some years after the original description and there is no evidence that the specimen from which it was made formed part of the original type series of *E. chrysogaster*. As against this, however, the description of the male style by Graham (1907) clearly shows that it was in fact *E. semisimplicipes* which he had before him when making his description of the male terminalia. On the other hand his description of the mesonotal markings as " Three parallel longitudinal narrow black bands run backward over the central portion, the median black band being continued to the scutellum by a band of golden scales " shows clearly that he relied for this part of his description on some of the specimens of the first species later found by Edwards in his type series. This description is that of a pale *E. chrysogaster*. One of Graham's ♀ in the British Museum fits it perfectly. It does not agree with the mesonotal markings of *E. semisimplicipes* which have been correctly described as " appearing almost black to the naked eye " (Van Someren, 1949) and " a soft pastel black to the naked eye. Under the microscope the scaling is seen to be mainly black with a powdering of yellow " (Haddow, 1946). From this I conclude that Graham undoubtedly took both *E. chrysogaster* (in Edwards' sense) and *E. semisimplicipes* into account in drawing up his description. Moreover I would consider that in choosing the former as the source of his lectotype Edwards gave fuller expression to Graham's intention than if he had chosen the latter. This despite the evidence of the figure of terminalia. In endeavouring to ascertain Graham's intention when describing *E. chrysogaster* attention is first directed to his key to species (Graham, 1907 : 86). This key is devoted solely to the separation of the four species which he is describing. No comparative study of other species appears to have been made. In it *E. chrysogaster* is separated from *E. oedipodius* and *E. leucopus* on characters of the head and prothoracic lobes which apply equally to both the forms confused by Graham under that name. The same is true of the feathering of the hind tarsus and the colour of the venter used for separation from *E. melanopus*. Turning to his description (*ibid.* : 157) it is found that the account of the male terminalia does not furnish differential characters. In particular the clasper (style) is similarly described in all four cases. As to whether Graham's later drawing may be taken to indicate a change in emphasis is beside the point. It appears to me that the only comparative character mentioned which we now know to offer a reliable distinction between *E. chrysogaster* and *E. semisimplicipes* is the ornamentation of the mesonotum and, as already indicated, Graham opted for *E. chrysogaster* (in Edwards' sense) as typical. Under *E. melanopus* the black scales on the mesonotum are noted as predominating in direct contradistinction to the condition described for *E. chrysogaster*. I have therefore accepted Edwards' lectotype as embodying to the largest possible extent the differential characters envisaged for *E. chrysogaster* by Graham. The genitalic characters now known to be specific to *E. semisimplicipes* were not recognised as significant by him and play no essential diagnostic part in his description.

I have been cautious in marking paratypes of this species since it seems that Edwards placed under *E. chrysogaster* certain specimens from the *E. melanopus* series sent by Graham (Edwards, 1911). I have, however, marked one ♀ from **Obuasi**, dated 15.xi.1907, as a paratype since it shows clearly the characteristic mesonotal ornamentation described by Graham for *E. chrysogaster* and would not, I think, have been placed by him under *E. melanopus*.

Eretmapodites quinquevittatus Theobald, 1901, *Monogr. Culic.* 1 : 280.

Theobald appears to have described this species from a series of 21 specimens, in the main collection at the British Museum, from Freetown, Sierra Leone, collected by Major E. E. Austen on various dates in August and September 1899. The British Museum has in addition some fragments on slides and one whole ♂ mounted in balsam which appears to be a typical *E. quinquevittatus* in the current sense of this name and is labelled as such by Theobald. Finally I found one well-marked *E. chrysogaster* ♀ dated 4.ix.99, in the duplicate collection. I do not think this was seen by Theobald as he makes no mention of the characteristic ornamentation of the mesonotum anywhere in his descriptions. *E. quinquevittatus* is the type species of the genus. Unfortunately the series on which Theobald based his description is mixed, comprising, so far as can be seen, 5 specimens (3 ♂ and 2 ♀) of *E. chrysogaster* Graham and 16 specimens of *E. quinquevittatus* in the sense in which these names are currently employed. Theobald marked 2 ♂ and 1 ♀ as types of *E. quinquevittatus* and, unhappily, chose all of them from the *E. chrysogaster* series. I have confirmed this by dissection of one of the ♂. Edwards (1911) reviewed the position and elected to ignore Theobald's type labels and to follow his description of the ♀ (that of the ♂ is based on *E. chrysogaster*). He justified himself in this by the assumption that Theobald was unaware that he was describing two species and was careless in his choice of types. I cannot agree with this assumption as there are three direct statements in Theobald's type descriptions (Theobald, 1901) which show that he knew that he had two species before him, culminating in a footnote (*ibid.* : 383) to the effect that the second species is to be described later under the name *E. austenii*. In his *Genera Insectorum* monograph (Theobald, 1905) Theobald had second thoughts. He says (p. 17), " There may be two species among the specimens in the British Museum, but the only difference I can detect is that some ♂s have no paddles and as these may have been rubbed off I have only definitely described one species, particularly as they were all collected in the same place." Finally (Theobald, 1910) he reverted to his original decision and described *E. austenii* marking a typical ♂ and a typical ♀ specimen of *E. quinquevittatus* (in the current sense) as the types.

Although disagreeing with Edwards in his interpretation of Theobald's intentions I am fully in agreement with him in his proposed course of action which was, as has been seen, to ignore Theobald's type labels, to follow his description of the ♀ type and (Edwards, 1941) to mark a ♀ lectotype. Edwards died before he could mark this lectotype and I have therefore marked one myself. We know from Austen (1904) that Theobald's type series contained at least four *E. chrysogaster* (one ♂ which has the tips of the hind tarsi missing probably being excluded) and three *E. quinquevittatus*, but it is not now possible to say with certainty which the latter were. It seems clear both from Austen's note and from Theobald's description that at least one was a well-marked ♀ and I have therefore chosen the best marked specimen from the five of this sex available to me. The data are " Wilberforce, Freetown, from larva, 24.ix.99."

While the choice of a specimen for lectotype is a fairly simple one, the justification for ignoring Theobald's labels and making this choice appears to me to require discussion at some length since serious matters of principle are involved. If Theobald's three cotypes (syntypes) are accepted and the choice of lectotype is limited to these then the name *E. chrysogaster* Graham must be sunk in the synonymy of *E. quinquevittatus*. This is highly undesirable since the species in question is one of at least suspected medical importance and it appears under Graham's name in a large body of scientific and entomological literature. To replace it by a name commonly attached to another (also fairly well known) species would in my view be rightly resented by applied entomologists. I do not maintain for a moment that the appeal to expediency could justify me in disregarding Theobald's type labels. Fortunately no such appeal is necessary since they can be disregarded on other more cogent grounds.

Theobald's choice of the name *quinquevittatus* clearly shows that he intended to describe a species having, to quote the first sentence of his description, " Thorax bright ferruginous brown, with six golden scaled lines, *dividing five darker ferruginous lines* " (italics mine). We now know that the specimen which he chose as his ♀ type cannot have possessed this character since it is an *E. chrysogaster* in which the mesonotum is never marked in this way. This would not, however, be apparent to Theobald since the specimen in question has the central area of the mesonotum very largely desquamated by rubbing. Apart from this the specimen is an exceptionally large and perfect one, by far the best of the females available to him. I am satisfied that it was solely for this reason that he chose it. There is absolutely no evidence whatever that it possessed any other special character which attracted his attention. Since this specimen fails to agree with his description in the one really distinctive feature which this embodies, and since by reason of the damage in question he cannot have been aware of this discrepancy I feel justified in treating his attachment of the type label as an involuntary lapse. I am quite certain that had the dorsal surface of the mesonotum been as perfect as the rest of the specimen he would never have chosen it as the type of his species and in consequence I feel justified in ignoring his type label and choosing a ♀ lectotype having the markings which he describes. It is interesting to note that both Banks (1908) and Edwards came to the same conclusion regarding Theobald's intention when both were much closer to Theobald than I (Edwards, 1911) and that Edwards felt himself justified on this ground in ignoring Theobald's type label although at that time there was none of the pressure from practical expediency which now exists.

The choice of a lectotype is now seen to lie between Theobald's two ♂ syntypes and his ♀ paratypes and it in fact resolves itself into a decision as to which sex Theobald would have chosen as his holotype and allotype respectively. As has been seen, Edwards, who was close to Theobald, unhesitatingly opted for the ♀ as holotype. This was, until quite recently, a common practice and probably reflects the greater importance, for medical purposes, of being able to recognise the ♀ than the ♂ and the fact that it is the ♀ which is most commonly taken in the adult state. To my mind, however, an even more cogent reason again lies in the choice of the name *quinquevittatus*. In his description Theobald states that "The thorax is not so distinctly ornamented as in the ♀". In point of fact the thorax of these ♂ does not show the " five darker ferruginous lines " at all. Under these circumstances would Theobald have used the name *quinquevittatus* if he had intended the ♂ rather than the ♀ to be taken as the type of the species? I think not, particularly when it is remembered that he had before him the excellent series of specimens later described as *E. austenii*, both sexes of which show the five lines equally distinctly. It seems to me apparent that had he regarded the male as the important sex he would have used the name *quinquevittatus* for this series and applied to the mixed series the name *austenii* which he had already chosen in honour of their collector. For all these reasons I have followed Edwards and, ignoring Theobald's type labels, have chosen one of the unmarked ♀ as hololectotype, marking it as such. I have marked as paratypes of *E. quinquevittatus* only the three specimens of *E. chrysogaster* chosen by Theobald as types (Theobald's type labels being, of course, left *in situ*). After carefully reviewing the evidence I do not feel justified in marking further paratypes since it is not clear which specimens were placed under *E. quinquevittatus*. Thus the remarks by Newstead (1907) discussed below might be taken to indicate that the type series of *E. austenii* included the unmarked ♀ of *E. chrysogaster*, while the dates of collection published for the former by Theobald (1910) suggest that some ♂ with unpaddled tarsi may have been placed in the type series of *E. quinquevittatus*.

As a final contribution to the solution of this problem it seems desirable to try to account for two anomalous statements by Theobald and Newstead respectively. In his original description of *E. austenii* (Theobald, 1910) Theobald quotes Newstead (1907) as stating that the presence of postnotal bristles is " quite evident in both *quinquevittata* and *austenii* in the ♀'s." In point of fact Newstead (*loc. cit.*) goes somewhat further than this and states categorically that they are absent from the ♂ of both species. Newstead's remark can, I think, only be accounted for by misobservation, particularly if it was based on specimens in the British Museum since the two *E. chrysogaster* ♂ marked by Theobald as types of *E. quinquevittatus* both clearly show them. Another possible inference, that these specimens were not at that time included in the type series, would further justify me in ignoring these males as possible lectotypes but I prefer not to stress this as I do not think that such an inference is in line with the rest of the evidence. The principal interest of the matter lies in the fact that it is precisely this character which would have enabled Theobald to sort his material correctly in the first place and that he did not go back to the type series of *E. quinquevittatus* to check it even after he had learned about it from Newstead. A similar frame of mind is also implied by Theobald's own inclusion of *E. quinquevittatus* in that part of his key to the genus (Theobald, 1910 : 559) which applies to species having narrow scales on the anterior pronotum. Such scales are not, of course, to be found in any of the specimens here discussed and the error can only be attributed to a complete failure on Theobald's part to refer back to the type series.

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A NOTE ON THE TRACHEAL SYSTEM OF THE MACHILIDAE.

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I. Introduction.

The Thysanura are generally recognised to be the most primitive of recent insects and no fossil insects are known that are more primitive. The order includes two suborders, the Archaeognatha, which have a mandible with a single cranial articulation, and the Zygentoma, which have a mandible with two cranial articulations.

Our knowledge of the tracheal systems of the Archaeognatha is based almost entirely on the work of Oudemans in 1887 (cited in Denis, 1949) and a few notes by Ŝulc (1927). It has been supposed by these writers that there are no connections between the tracheal system of one segment and that of another, or between the tracheal systems of right and left sides. It is here shown that neither of these suppositions is correct.

2. Material and Methods.

The species used in this work were *Petrobius brevistylis* Carpenter, collected at Portishead, Somerset, and *Dilta hibernica* Carpenter, collected in Leigh Woods, Bristol. A modification of the cobalt napthenate vacuum method of Wigglesworth (1950) was used to inject the trachea. After injection the specimens were fixed in Carnoy's fluid, dehydrated and cleared in xylol. The legs of the specimens were removed to facilitate examination of the ventral aspect of the thorax. Six preparations of *Petrobius brevistylis*, and four of *Dilta hibernica* were made. Microphotographs of the preparations were taken at different levels.

3. Tracheal Systems.

The tracheal systems of the two species do not differ in any important particular. As pointed out by previous writers, spiracles are present on the meso- and metathorax, and on the abdominal segments two to eight. Tranverse connections near the ventral surface of the prothorax and mesothorax were present between the mesothoracic tracheal trees of right and left sides. Longitudinal connections between the meso- and metathoracic tracheal trees of one side were also present (figs. 1–2). In the preparations of *Petrobius brevistylis*, a transverse connection in the prothorax was present in every preparation made, but the transverse connection in the mesothorax was only present in two preparations and was incomplete in a third. The longitudinal connection was present in three preparations, was absent in one, and could not be determined in two preparations due to faulty injection.

The absence of transverse and longitudinal connections between the tracheal trees in the abdomen, and the supposed absence of such connections in the thorax,

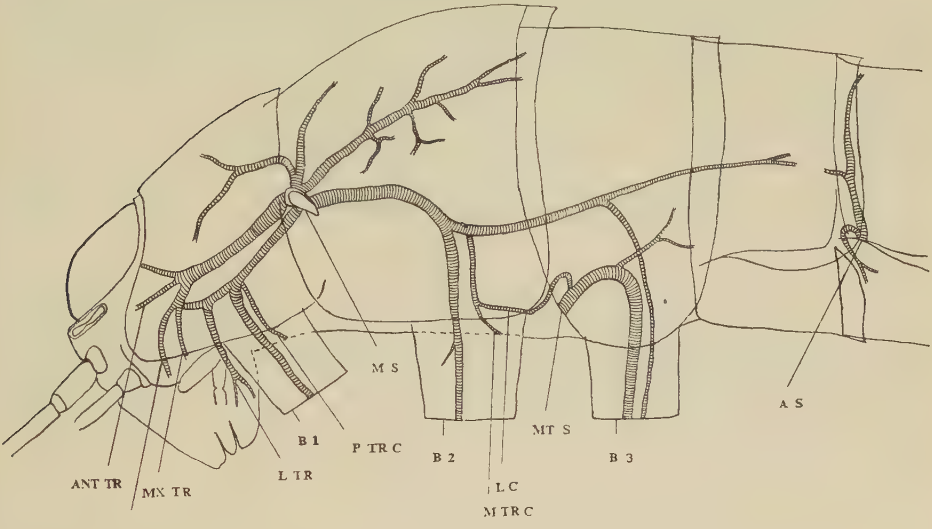

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FIG. 1.—*Petrobius brevistylis* Carpenter. Diagram of tracheal system of thorax, lateral view. *b.1.*, *b.2.*, *b.3.*, Bases of legs; *m.s.* mesothoracic spiracle; *mt.s.* metathoracic spiracle; *a.s.* 1st abdominal spiracle; *p.tr.c.* prothoracic transverse connection; *m.tr.c.* mesothoracic transverse connection; *l.c.* longitudinal connection; *ant.tr.* antennary trachea; *md.tr.* mandibular trachea; *mx.tr.* maxillary trachea; *l.tr.* labial trachea.

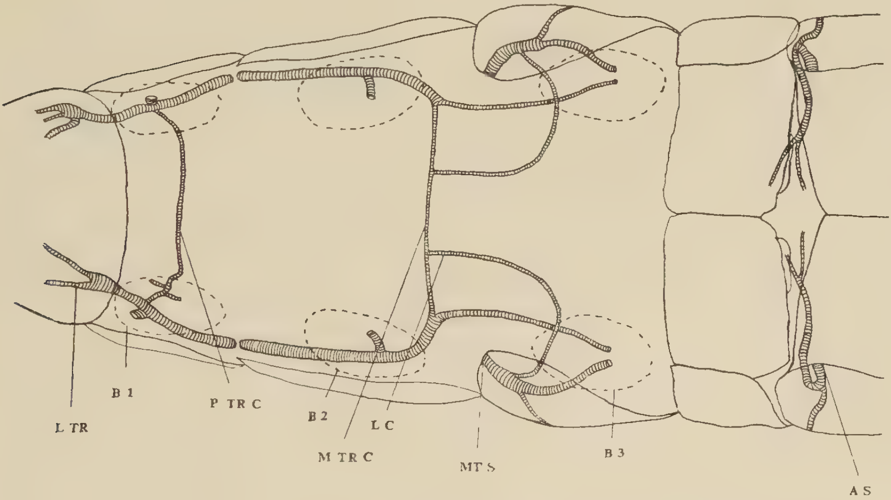

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FIG. 2.—*Petrobius brevistylis* Carpenter. Diagram of tracheal system of thorax, ventral view. Lettering as for fig. 1

has been assumed to be secondary by Denis (1949). However, there is every reason to suppose that the tracheal system of the Machilidae is a primitive one and not derived from a system like that of the suborder Zygentoma. The fact that the longitudinal and the posterior transverse connections are only established in some specimens is of particular interest.

4. ACKNOWLEDGMENT.

I should like to thank Dr. H. E. Hinton for suggesting the problem and for his help with it.

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LECTOTYPES OF MOSQUITOES (DIPTERA : CULICIDAE) IN THE BRITISH MUSEUM.

Part II. Genera *Toxorhynchites*, *Aëdes* (Subgenera *Aëdimorphus*, *Banksinella*), *Culex* (Subgenera *Neoculex*, *Culiciomyia*, *Mocthogenes*, *Culex*).

By P. F. Mattingly, B.Sc., F.R.E.S.
(*British Museum* (*Natural History*).)

The present paper is the second of a series designed to validate lectotypes in the British Museum by publication. It deals mainly with Ethiopian species described by Edwards (1941) of which the types had not been marked by him at the time of his death. References not included in the bibliography to the present paper will be found in the first paper of the series (Mattingly 1955).

Oriental Species.

Genus *CULEX* Linnaeus.

Culex (*Culex*) *mimeticus* var. *mimuloides* Barraud, 1924, *Indian J. med. Res.* **11** : 992.

Edwards (1934) raised this variety to specific rank. He records it from Ootacamund (*Fletcher*, *Puri*), Coonoor (*Puri*), Kodaikanal (Palni Hills, *Patton*) and unnamed localities in the Nilgiri Hills (*Kazan Chand*). Barraud did not mark types. His original description refers specifically to material from the Nilgiri Hills and from this it is inferred that Patton's specimens (which are in the British Museum and are undated) cannot have formed part of the type series. Puri's specimens were collected in 1928, four years after the type series was described. Fletcher's specimens were collected in 1913 and were mentioned by Edwards (1921 : 338) in his revision of the Palearctic mosquitoes. Barraud (1924) states that he has not seen the specimens mentioned in this revision. It thus seems clear that the type series is the one collected by Khazan Chand and presented to the British Museum by Barraud, and since this fits all the data given by Barraud, I have marked a ♂ from it as the hololectotype, a ♀ as the allolectotype and the remaning 11 ♂ and 12 ♀ as paratypes. The hololectotype is numbered 1484 and has associated terminalia on a slide as have 5 of the ♂ paratypes, numbers 1442, 1483, 1485, 1486 and 1489 respectively. Data for the whole series are " Nilgiri Hills, x.1915, Khazan Chand."

Culex tritaeniorhynchus var. *siamensis* Barraud & Christophers, 1931, *Rec. Malar. Surv. India* **2** : 283.

Barraud and Christophers do not appear to have marked types. The British Museum has four ♂ from the type series with terminalia on slides. These are probably the ones stated by Barraud and Christophers (1931) to have been sent to Edwards. I have marked one, numbered Y.454, as the hololectotype and the other three as paratypes. Data for the hololectotype and one paratype (No. Y.460) are " Chiengmai, Siam, 17.xii.30, J. A. Sinton ". Data for the other two paratypes (Nos. Y.376 and Y.381) are " Phya Thai Hotel, Bankok, Siam, xii.1930, J. A. Sinton)."

PALAEARCTIC SPECIES.

Genus *THEOBALDIA* Neveu-Lemaïre.

Culicella morsitans var. *litorea* Shute. 1928, *Entomologist* **61** : 186.

Shute did not mark types. The original description refers only to material collected in January, 1928. The British Museum has specimens marked as collected in the type locality by Shute in March and May of that year and one slide of terminalia without date. Shute informs me that all this material was taken into account in drawing up his description and therefore forms part of the type series. I have accordingly chosen a ♂ hololectotype and a ♀ allolectotype and have marked the remaining specimens as paratypes. Data for the holo- and allotype are " Walton-on-the-Naze, Essex, v.1928, P. G. Shute ". Among the paratypes, 2 ♂, 4 ♀, 4 whole larvae, 2 ♂ heads on slides and one set of ♂ terminalia have the same data. Two whole larvae were collected in March and one ♂ and one ♀ adult in April instead of in May, 1928 and one set of ♂ terminalia on a slide is undated.

Genus *TOXORHYNCHITES* Theobald.

Megarhinus erythrurus Edwards, 1941, *Mosq. eth. Reg.* **3** : 30.

Described from 3 ♂ and 3 ♀ from NIGERIA : Ibadan, 22.viii.1929 (*H. W. Kumm*); 1 ♀, same locality, 20.vi.1913 (*W. A. Lamborn*); 2 ♀, Lagos, undated, (*J. Cauchi*). I have marked one of Kumm's ♂ as the hololectotype and the other specimens as paratypes.

Genus *AËDES* Meigen.

Subgenus *AËDIMORPHUS* Theobald.

Aëdes (*Aëdimorphus*) *kapretwae* Edwards, *ibid.* : 162.

Described from 9 ♂ and 16 ♀ from KENYA : Mt. Elgon, v. 1939 (*T. H. E. Jackson*). I have marked one of the ♂ as the hololectotype and one of the ♀ as allolectotype. I have marked the remaining specimens as paratypes. One paratype of each sex has been presented to the United States National Museum in exchange for other material.

Aëdes (*Aëdimorphus*) *tricholabis* Edwards, *ibid.* : 179.

Described from 2 ♂ and 2 ♀, KENYA : Gede, 1940 (*E. C. C. Macdonald*). I have marked one of the ♂ as hololectotype and the other specimens as paratypes.

Aëdes (*Aëdimorphus*) *abnormalis* ssp. *kabwachensis* Edwards, *ibid.* : 181.

Described from 1 ♂ and 8 ♀ and two sets of ♂ terminalia from KENYA : Kabwach, undated (*C. Teesdale*). I have marked the ♂ as hololectotype and the remaining specimens as paratypes. The ♂ is numbered 44. This and 4 of the ♀ paratypes are accompanied by liaison larval and pupal pelts. One ♀ paratype has been presented to the United States National Museum in exchange for other material.

Aëdes (*Aëdimorphus*) *wigglesworthi* Edwards, *ibid.* : 182.

Described from 5 ♂ and 2 ♀ from NIGERIA : Sapele, vi.1928. (*V. B. Wigglesworth*) and 1 ♂ from NIGERIA : Ebute Metta, near Lagos, 29.vii.1929 (*C. B. Philip*). I have marked one of the ♂ from Sapele as hololectotype and the other specimens as paratypes. Edwards (1941 : 394) also described the pupa of this species from three pelts which were until recently in the collection of the London School of Hygiene. It appears to me that his description may reasonably be construed as forming part of the type description since it was published in the same work and only appears on a later page for formal reasons. The late Professor P. A. Buxton very kindly presented the three pelts to the British Museum, and I have marked them as paratypes. At the same time he also presented a whole larva collected by Wigglesworth in the type locality. So far as I am aware this is the only specimen of the larva in existence. It is possibly the one figured by Wigglesworth (1929, reproduced in Hopkins 1936, 1952), but this is uncertain. In any event it clearly played no part in Edwards' description and accordingly I have left it unmarked.

Aëdes (*Aëdimorphus*) *cumminsi* ssp. *holocinctus* Edwards, *ibid.* : 193.

Described from a unique ♂ from KENYA: Gede, 1940 (*E. C. C. Macdonald*). I have marked this as the holotype.

Aëdes (*Aëdimorphus*) *hirsutus* var. *adenensis* Edwards, *ibid.* : 198.

Edwards cites as the type series 1 ♂ and 8 ♀ from W. ADEN PROTECTORATE : Jebel Jihaf, 7100 ft., ix.1937 (*Scott & Britton*). In fact, however, there are 10 specimens in the type series with the following data: 2 ♀, Jebel Jihaf, *c.* 7100 ft., –.x.1937 (*H. Scott & E. B. Britton*) and 1 ♂ and 7 ♀, W. ADEN PROTECTORATE: Dhala, 4800 ft., 14.ix.1937 (*H. Scott & E. B. Britton*). Since the critical factor, if any, is likely to be altitude I have marked one of the ♀ from Jebel Jihaf as the hololectotype and the ♂ from Dhala as allolectotype. The other specimens I have marked as paratypes.

Aëdes (*Aëdimorphus*) *leesoni* ssp. *verna* Lewis, 1944, *Proc. R. ent. Soc. Lond.* (B) **13** : 27.

Described from holotype ♀ with associated (paedotype) larval and pupal pelts and 3 ♂ paratypes from SUDAN : Danagla Forest, 22.viii.1943 (*D. J. Lewis*) and 7♂ and 3 ♀ paratypes from SUDAN : Wad Medani, 11–12.ix.1943 (*D. J. Lewis*). It was stated that the holotype and some paratypes would be sent to the British Museum, but owing to the war this was not done. Dr. Lewis has now kindly sent the holotype ♀ and a ♂ from Danagla Forest marked by him as allotype. The ♂ has no terminalia, but it is hoped that these, together with the paedotype pelts and some further paratypes, will be sent later.

Aëdes (*Aëdimorphus*) *eritreae* Lewis, 1942, *ibid.* **11** : 165.

Described from 11 ♀ and 4 ♂ from ERITREA: Acchele Guzai, "27.iv.42 (including types) and 30.iv.42". Dr. Lewis has kindly sent a ♀ dated 27.iv.1942 and a ♂, without terminalia, dated 30.iv.1942. The holotype has not yet been marked. I have marked the ♀ as a cotype and the ♂ as a paratype pending the receipt of further material which has been promised.

Subgenus *Banksinella* Theobald.

Aëdes (*Banksinella*) *flavimargo* Edwards, 1941, *Mosq. eth. Reg.* **3** : 209

Described from 2 ♀ from Kenya: Gede, undated (*E. C. C. Macdonald*). I have marked one of these as the hololectotype and the other as a paratype.

Aëdes (*Banksinella*) *ellinorae* Edwards, *ibid.* : 212.

Described from 2 ♂ and 12 ♀ from Kenya: Gede, undated (*E. C. C. Macdonald*). I have marked one of the ♂ as hololectotype and the remaining specimens as paratypes.

Genus *CULEX* Linnaeus.

Subgenus *Neoculex* Dyar.

Culex (*Neoculex*) *subrima* Edwards, *ibid.* : 262.

Edwards himself marked the holotype. His type series contained 2 ♂ from Belgian Congo: Stanleyville, viii–ix.1928 (*J. Schwetz*). I have only one specimen with these data, but the series in the British Museum also contains another ♂ from Stanleyville without data as to collector or date. The series is also said (Edwards, 1941) to have contained 3 ♂ from Belgian Congo: Pawa, 28.v.1938 (*Dr. Radna*). I have these and I have marked all 5 specimens as paratypes. I have also 3 further ♂ from Pawa, viii.1938, (*Radna*), but Edwards does not mention these so I have left them unmarked.

Culex sunyaniensis Edwards, *ibid.* : 263.

Edwards marked as holotype a ♂ from Gold Coast: Sunyani, 1915. I have also another ♂ with identical data and 2 dissected ♂ from Sudan: K. (? Khor) Namburi and an undecipherable locality, 1911 (*H. H. King*) and one from Sudan: Meridi, 5.xii.1936 (*W. Ruttledge*) respectively. I presume that the first two are specimens mentioned by Edwards from Upper White Nile, Sudan, and I have marked all three as paratypes. A dissected ♂ from Sudan: Yei, 21.xii.1935 is not mentioned by him and I have left it unmarked. I have marked as paratypes two dissected ♂ from Nigeria: Lagos, undated (*S. L. M. Connal*) and Gold Coast: Koforidua, vii.1919 (*F. H. Storey*). ♀ and undissected ♂ from these localities I have left unmarked as Edwards does not appear to have wished to include them in the type series. I have not been able to find the pupal pelts described by Edwards (1941 : 411). I have marked the whole pupae which he described as paratypes.

Culex (*Neoculex*) *wigglesworthi* Edwards, *ibid* : 264.

Edwards himself marked the holotype. I have marked the 4 other ♂ and 1 ♀ with data detailed by him as paratypes. A dissected ♂ from Belgian Congo: Thysville (*J. Schwetz*), I have left unmarked as Edwards does not mention it.

Culex (*Neoculex*) *albertianus* Edwards, *ibid*, : 265.

Edwards himself marked the holotype. The head and pharynx are on a slide. It is undated. I could find only one of the ♂ from Kericho which he mentions and this I have marked as a paratype. It is dated xii.1938.

Culex (*Neoculex*) *calabarensis* Edwards, *ibid* : 265.

Edwards marked the holotype. I have marked the other two ♂ which he mentions as paratypes. The specimens from Calabar are dated 18.vi.1910 and the one from Forcados 26.vi.1910.

Culex (*Neoculex*) *galliardi* Edwards, *ibid* : 266.

Edwards marked the holotype. I have marked the other 3 specimens which he mentions as paratypes. He does not state the dates. These are Forcados, 18.vi.1910, Coquilhatville, 20.x.1910, Bap, 21.v.1925, Onitsha, iv.1928.

Culex (*Neoculex*) *adersianus* Edwards, *ibid.* : 268.

Described from 2 specimens. I have marked the specimen from Mombasa as the holotype, in accordance with the intention which he expresses and the specimen from Zanzibar as a paratype. The date on the holotype is ix.1924. The paratype is undated.

Culex (*Neoculex*) *acrostichalis* Edwards, *ibid.* : 268.

Edwards did not mark the type. I have marked one of the 3 ♀ from Kasala as hololectotype and the other 2 specimens from this locality and the specimen from the Sudan which he mentions as paratypes. I can only find two of the specimens from Kampala, and one of these is represented by a slide of head and pharynx only. It is undated. The whole specimen is dated 21.x.1926. I have marked both as paratypes.

Subgenus *Culiciomyia* Theobald.

Culex (*Culiciomyia*) *subaequalis* Edwards, *ibid.* : 276.

Edwards marked the holotype. I have marked the other specimen which he mentions as a paratype.

Subgenus *Mochthogenes* Edwards.

Culex (*Mochthogenes*) *simpliciforceps* Edwards, *ibid.* : 279.

The British Museum has all 5 specimens listed by Edwards. The 3 ♂ are all dissected. I have marked 1 ♂, UPPER WHITE NILE : Bundle to Hierallah, 19.iii.1911 (*H. H. King*) as hololectotype. The other ♂ from this locality has the same date. The 2 ♀ are dated 29.iii.1911 (Aow River) and 2.iv.1911 (Khor Namlini). The ♂ from Arua is dated 7.vii.1932. I have marked these 4 specimens as paratypes. The hololectotype bears the number 1013.

Subgenus *Culex* Linnaeus.

Culex (*Culex*) *aurantapex* var. *jinjaensis* Edwards, *ibid.* : 293.

The British Museum has a series of 7 ♂ and 7 ♀ from the type locality. Edwards did not mark the type. I have marked a ♂ dissected by him as hololectotype and the remaining specimens as paratypes. The holotype is dated 10.xi.1930 and the paratypes have various dates in the same year. All were collected by *G. H. E. Hopkins*. The British Museum also has a ♂ from KAMPALA: 5.ii.1930 (*G. H. E. Hopkins*) and I have marked this as a paratype.

Culex (*Culex*) *striatipes* Edwards, *ibid.* : 311.

Described from 3 specimens only. Edwards did not label the holotype, but his designation leaves no possible doubt as to the specimen intended. I have accordingly marked it. I have marked the accompanying ♂ from Mt. Elgon and ♀ from Nairobi as paratypes.

Culex (*Culex*) *terzii* Edwards, *ibid.* : 312.

Edwards marked the holotype. I have marked a series of specimens from Salisbury and Bindura and 2 ♀ from Waterval Boven as paratypes. The holotype is dated April, 1900.

Culex (*Culex*) *umbripes* Edwards, *ibid.* : 321.

As noted previously (Mattingly & Lips, 1953), Edwards failed to mark the type. I have therefore marked one of the two specimens examined by him as hololectotype and the other as a paratype. The British Museum also has a third specimen with identical data which Edwards appears to have overlooked. I have left this unmarked. The type locality is misspelt on the data labels. The correct rendering is discussed by Mattingly & Lips (1953) under *Aëdes leptolabis* Edwards.

Culex (*Culex*) *trifilatus* ssp. *aenescens* Edwards, *ibid.* : 323.

Described from 3 ♂ and 2 ♀ from UGANDA: Kameranjoka (*G. H. E. Hopkins*). I have marked one of the dissected males, dated 18.ix.1931, as hololectotype and the other specimens as paratypes. The latter include a dissected ♂ dated 18.ix.1931, an undissected ♂ with the same date, a ♀ dated 8.ix.1931 and another ♀ dated 16.ix.1931. I have marked the pupal pelts described by Edwards (1941 : 421) as paratypes.

Culex (*Culex*) *andersoni* ssp. *bwambanus* Edwards, *ibid.* : 325.

Described from a unique ♂ which I have marked as the holotype. The data are as given by Edwards (1941).

Culex (*Culex*) *andersoni* ssp. *abyssinicus* Edwards, *ibid.* : 325.

Described from 5 ♂ from ABYSSINIA: Addis Ababa, various dates in April, 1936 (*J. W. S. Macfie*). One of these is dissected and I have marked it as hololectotype. It is dated 18.iv.1936. I have marked the other specimens as paratypes. I have also marked as paratypes 3 dissected ♂ from the same locality, dated i.1927, (*H. Scott*), 1935 (*H. Sharp*), and 24.xii.1935 (*C. E. Bevan*), one dissected ♂, 1 undissected ♂ and 1 ♀ from ABYSSINIA: Dessie, 1936 (*C. E. Bevan*), 2 ♀ from the same locality, 21.iii.1936 (*J. W. S. Macfie*), 2 ♀ from ABYSSINIA : Koram, iii.1936 (*J. W. S. Macfie*), 1 dissected ♂ from L. Ashangi, 1936 (*C. E. Bevan*) and 1 undissected ♂ and 1 ♀ from ABYSSINIA :

Maji, vii.1928 (*P. Holland*). The British Museum also has a dissected ♂ from Abyssinia: Mulu, 19–21.xii.1926 (*H. Scott*) but Edwards does not mention this, so I have left it unmarked.

Culex (*Culex*) *vansomereni* ssp. *elgonicus* Edwards, *ibid.* : 328.

Described from 2 dissected ♂ and 1 ♀ from Buginyanya, 15.viii.1929 (*G. R. L. Hancock*). I have marked one ♂ as the hololectotype and the other two specimens as paratypes.

Culex (*Culex*) *vansomereni* ssp. *toroensis* Edwards and Gibbins, 1939, *Ruwenzori Expd.* **1** : 32.

Described from 3 dissected and 2 incomplete ♂ and 1 ♀ from Uganda: Kisomoro, 20.vi.1936 (*F. Shillito*) and 9 ♂ and 9 ♀ from Kararama Camp, Namwamba Valley, 5.i.1935 (*E. G. Gibbins*). I have marked one of the dissected ♂ from Kisomoro as hololectotype and the remaining specimens as paratypes.

Culex (*Culex*) *vansomereni* ssp. *macrophyllus* Edwards and Gibbins, *ibid.* : 31.

Described from 5 dissected ♂ and 4 ♀ from Lugezi Camp between Mt. Mgahinga and Mt. Sabinio, xi.1934 (*F. W. Edwards*). I have marked one of the ♂ as hololectotype and the other specimens as paratypes. I have left unmarked an undissected ♂ from Mt. Sabinio, 29.xi.1934 (*F. W. Edwards*) since this seems to have been collected somewhat below the type locality and is not mentioned by Edwards in his description.

Culex (*Culex*) *chorleyi* Edwards, 1941, *Mosq. eth. Reg.* **3** : 330.

The British Museum has 2 dissected and 1 undissected ♂ from the type locality. I have marked one of the former as hololectotype. It was previously marked by Hopkins as the paedotype of *Culex pallidocephalus* Theobald and has an associated larval skin, much damaged by dessication of the mountant, which I have marked as part of the holotype. I have marked the two other specimens as paratypes. Their dates are 3.ix and 5.ix.1932. The date on the hololectotype is 3.ix.1932. I have also marked as paratypes 7 ♀ and 5 ♂ from Kampala (*Hopkins*), 1 ♂ from Belgian Congo : Nyangezi, 1939 (*J. Schwetz*) and 5 ♀ and 2 ♂ from Belgian Congo: Kabare, viii–ix.1939 (*J. Schwetz*) as paratypes. Finally I have marked as paratypes the 5 pupal pelts, 3 from Masaka and 2 from Kampala, described by Edwards (1941 : 423).

Culex (*Culex*) *invidiosus* var. *vexillatus* Edwards, *ibid.* : 339.

Described from 5 ♂, 3 of them dissected, and 1 ♀ from Uganda: Kampala (*G. H. E. Hopkins*). I have marked one dissected ♂, dated 24.ii.1930, as hololectotype and the other specimens, which are dated 20 and 21.xii.1929, as paratypes. I have also marked 2 ♂ and 2 ♀ from Nigeria, Ibadan, 30.viii.1929 (*C. B. Philip*), 1 ♂ and 1 ♀ from Belgian Congo, Stanleyville, v–vii.1928, (*J. Schwetz*), 5 ♂ and 1 ♀ from Belgian Congo, Popokabaka, undated (*J. Schwetz*) and 4 ♂ from Belgian Congo: Léopoldville (*C. Henrard*) as paratypes. Edwards also saw 2 ♂ from Belgian Congo : Masua, 11.ix.1929 (*J. Schwetz*) and dissected one of them, but I have not marked these, since he does not mention them.

Culex (*Culex*) *guiarti* var. *sudanicus* Edwards, *ibid.* : 345.

Described from 6 ♂ from Gold Coast : Bole, 1911 (*A. Ingram*) and 2 ♂ and 1 ♀ from Nigeria : Gadau, 1931 (*A. W. Taylor*). One of the undissected ♂ from Bole is dated 22.viii.1911. The others are marked only with the year. Two of them are dissected and I have marked one of these as the hololectotype. Of the specimens from Gadau one ♂ is marked only with the year. The others are dated –.viii.1931. I have marked all the specimens, other than the hololectotype, as paratypes.

Culex (*Culex*) *weschei* ssp. *gediensis* Edwards, *ibid.* : 345.

Described from 6 ♂ and 5 ♀ from Kenya : Gede (*E. C. C. Macdonald*). Of these I have been able to find only 4 ♂ and 2 ♀. They are undated. Two of the ♂ are dissected and I have marked one of these as hololectotype. I have marked the remaining specimens as paratypes.

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THE INFLUENCE OF TEMPERATURE ON DIAPAUSE DEVELOPMENT IN THE DRAGONFLY *LESTES SPONSA* (HANSEMANN) (ODONATA: LESTIDAE).

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Introducion.

In England *Lestes sponsa* (Hansemann) is univoltine. Oviposition occurs from early July to early September; the eggs overwinter and hatch in April of the following year; larval development is completed in 2–3 months and emergence usually begins in late June (Corbet, 1953). The pattern of this life-history, and the fact that hatching of the eggs in April is well synchronised, indicate that the egg is a diapause stage. In 1952–53 preliminary experiments were undertaken to investigate the effects of temperature upon the completion of diapause development.

Material and Methods.

On 1st July, 1952, a female *L. sponsa* was seen ovipositing in stems of *Eleocharis palustris* (L.) at the Fish Pond, Wokefield Common, Berkshire. These stems were marked and left *in situ*. On 17th July they were collected and thereafter kept at room temperatures (*ca.* 20° C.) until 13th August, when 20 eggs were removed from the plant tissue. In all of these blastokinesis had been completed and the embryos possessed differentiated appendages. It was known from previous culture of eggs of *L. sponsa*, *Aeshna grandis* (L.) and *Sympetrum danae* (Sulzer) that embryos completed blastokinesis and attained an advanced stage of morphological development in about two weeks after laying, and were therefore all in this condition before the onset of diapause (Corbet, *unpublished observations*). Thus, by leaving the eggs of *L. sponsa* at about 20° C. for 27 days after collection, it could be confidently assumed that all would have reached a similar stage of development. This step made allowance for any oviposition which might have occurred in the plant stems between 1st and 17th July. All the eggs used in this experiment may, therefore, be considered to have completed normal pre-diapause development and, in the terminology of Church and Salt (1952), may be called " mature diapause eggs."

The stems were cut into short pieces containing known numbers of eggs, and these were placed in glass tubes (3 × 1 inches) containing tap water. The tubes were floated in constant-temperature water-tanks and subjected to natural photoperiods throughout the experiment. Temperature in the tanks did not depart from required values by more than one quarter degree Centrigrade. The experiment was begun on 13th August, 1952, and concluded on 30th June, 1953.

Mature diapause eggs were subjected to three main types of treatment:

- (A) Kept at 20° C. throughout.
- (B) Five sets: subjected to 10° C. for 3, 6, 9, 12 or 15 weeks before being returned to 20° C.
- (C) Five sets: subjected to 5° C. for 3, 6, 9, 12 or 15 weeks before being returned to 20° C.

RESULTS.

The times taken for eggs to hatch after being placed in 20° C. are given in Table I and figure 1. It can be seen that eggs fall into one of two categories: in the first, hatching occurred after 4–28 days and, in the second, after 90–217 days. The separation between these groups was quite distinct, and it is con-

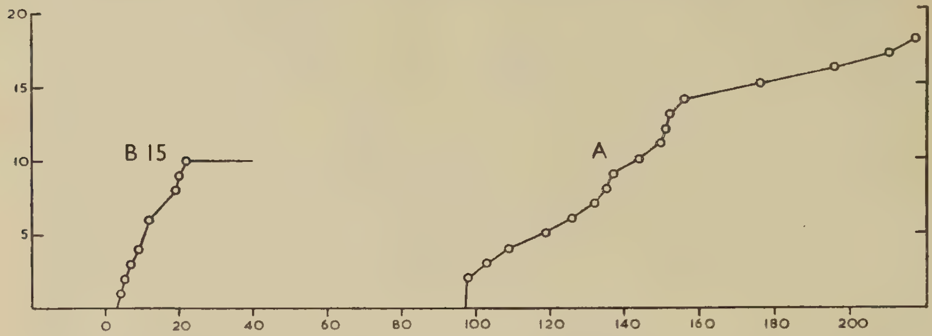

FIG. 1.—Time-distribution of hatching of eggs in which diapause development had been completed (group B, 15) and in which it had not (group A). *Abscissa:* days after first exposure to 20° C. *Ordinate:* cumulative number of eggs hatching.

TABLE I.—*The effects of temperature on completion of diapause development in mature diapause eggs.*

Group.	Treatment.	Number of eggs to hatch and (days before hatching) in which, when first subjected to 20° C., diapause development was:		Total eggs.
		Complete.	Incomplete.	
A	Subjected to 20° C. throughout	.	18 (98, 98, 103, 109, 119, 126, 132, 135, 137, 144, 150, 151, 152, 156, 176, 196, 210, 217)	25
B	Previously subjected to 10° C. for . . . weeks before return to 20° C.			
	(3)	.	5 (133, 153, 163, 175, 189)	10
	(6)	.	1 (103)	10
	(9)	.	.	10
	(12)	1 (24)	1 (90)	10
	(15)	10 (4, 5, 7, 9, 12, 12, 19, 19, 20, 21)	.	14
C	Previously subjected to 5° C. for . . . weeks before return to 20° C.			
	(3)	Eggs accidentally destroyed		10
	(6)	.	.	10
	(9)	.	5 (95, 103, 111, 121, 127)	10
	(12)	.	.	10
	(15)	2 (5, 28)	3 (135, 156, 156)	14
			Total .	133

sidered that the first comprised eggs which had completed diapause development before being placed in 20° C., and the second those which had not. Results have been tabulated according to this interpretation.

In only three experimental sets did any eggs complete diapause development before being returned to 20° C. Of these, group B, 15 weeks, showed the highest proportion (71 per cent.) of completion. From figure 2 it appears that diapause development proceeds most rapidly at a temperature near to 10° C., and that probably all eggs would have completed diapause development after 18 weeks of exposure to this temperature.

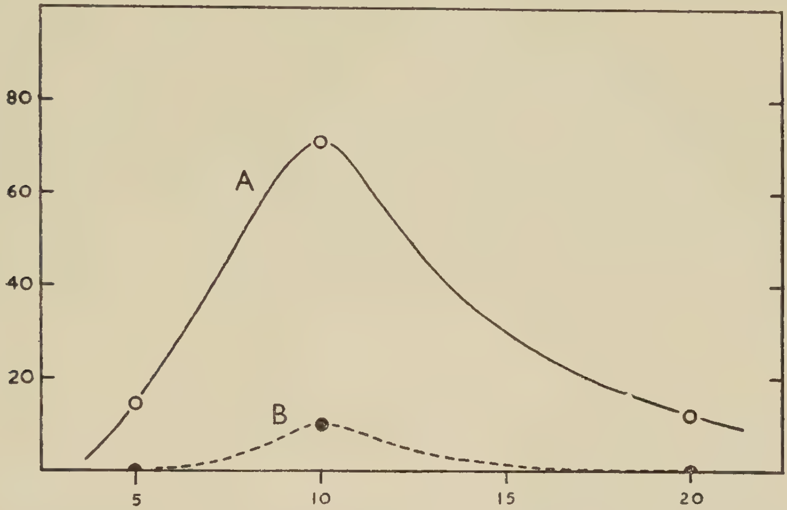

Fig. 2.—Completion of diapause development at different temperatures. *Abscissa :* temperature in degrees Centigrade. *Ordinate :* percentage of eggs to have completed diapause development at a given temperature during : A : 15 weeks ; B : 12 weeks.

Diapause cannot be intense, since it was completed slowly at 20° C. by 72 per cent. of eggs. In this respect, temperature requirements for the completion of diapause development may be somewhat similar to those of *Anax imperator* Leach (Corbet, 1956).

The principal difference between those eggs which completed diapause development at 5 or 10° C. and those which did so at 20° C. lies not in the total period spent in the egg before hatching, but in the synchronisation of hatching (*see* fig. 1).

DISCUSSION.

These experiments establish the existence of an obligate diapause in the egg of *L. sponsa,* and suggest that diapause development proceeds most rapidly at a temperature below the lower threshold for hatching (10–20° C.). Thus, in nature, it is probable that diapause development proceeds rapidly in late autumn, but is completed before temperatures fall to 5° C ; in the following spring, when temperatures rise high enough to permit post-diapause development, synchronised hatching occurs.

Diapause in *L. sponsa* can be seen as a mechanism ensuring that all individuals pass the winter in the egg, which may perhaps be the stage best able to resist cold. It thus serves a very different function from the diapause in *A. imperator*, which is developed in the final larval instar and is responsible for synchronising emergence of the adult (Corbet, 1954).

SUMMARY.

1. An obligate diapause exists in the egg of *Lestes sponsa*, and experiments have been conducted to determine the influence of temperature on the rate of diapause development.

2. The optimum temperature for diapause development lies near to 10° C.; at this temperature, 71 per cent. of eggs completed diapause development in 15 weeks, 10 per cent. in 12 weeks and 0 per cent. in 9 weeks or less. At 20° C. diapause development proceeds slowly, taking from 14–31 weeks.

3. The lower threshold permitting hatching of eggs lies between 10 and 20° C. At 20° C., hatching of eggs in which diapause development has been completed previously at 5 or 10° C. is temporally compressed and occurs after about 2 weeks.

ACKNOWLEDGMENTS.

I am indebted to Professor V. B. Wigglesworth and Dr. A. D. Lees for advice and criticism and to Mr. R. Holder for technical assistance. I am grateful to the Department of Scientific and Industrial Research for a maintenance allowance while the work was in progress.

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ON THE DIPTERA ASSOCIATED WITH THE STINKHORN (*PHALLUS IMPUDICUS* PERS.) WITH NOTES ON OTHER INSECTS AND INVERTEBRATES FOUND ON THIS FUNGUS.

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It has long been known that fruiting bodies of the Stinkhorn fungus (*Phallus impudicus* Pers., Basidiomyceti) are very attractive to flies, but little work has been done to establish the exact nature of the relationship between fungus and insect. Usually it has been assumed that the flies are mainly attracted to the gleba on which they feed, and N. A. Cobb (1906 : 44 *et. seq.*) has shown that spores from the gleba of the related *Ithyphallus coralloides* Cobb, an Hawaiian species, pass uninjured through the digestive tract of flies, which suggests that these insects are an important factor in spore distribution.

Collart (1950 : 5), from the high proportion of females to males found on a specimen of *P. impudicus* in Belgium, suggested that oviposition, not feeding, is the major attraction to flies and Parmenter (1951) supported this view from observations made in England. Unfortunately neither author had the opportunity of breeding adults from the fungus and the literature yielded no records to support their theory. Luther (1946) gives a brief list of Arthropods found on this fungus in Finland, which includes seven Diptera, none of which were bred. A large colony of *P. impudicus* provided an opportunity to investigate this problem and it was found that in its various stages of growth the fungus attracts some species of flies for feeding and some for ovipositing. This colony was situated beneath a hedge close to dead tree stumps and partly under Rhododendrons along the drive of the National Agricultural Advisory Service, West Midland Provincial Headquarters, Wolverhampton, Staffordshire. Prof. G. C. Varley tells me that he has also noticed a Stinkhorn colony beneath Rhododendrons. It is probable that the thick deposit of dead leaves beneath the shrubs provides a suitable habitat.

Many fungi were present in the " egg " stage (*vide* Ramsbottom, 1953 : 179) and it was found that a fruiting body would emerge overnight and last for two to three days, by which time the nocturnal feeding of slugs had broken it into pieces. The slimy green gleba, containing the spores, was usually removed by flies during the first day of fruiting ; if the day was sunny, after a few hours all the gleba had gone. Even with the gleba removed flies were still attracted as long as the odour remained. Some species could be found on very old fungi and some were found on fungi in the " egg " stage. It is these two groups of species which would appear to be attracted for purposes of oviposition and, as will be seen below, certain of these or related species were bred from the fungus.

Flies Visiting the Fungus.

The species of flies visiting the fungus depends upon the date when the fruiting body appears, the locality and habitat. The flies visiting a fruiting body in the main colony on 29th September were mainly *Sarcophaga* spp., but a fungus placed near buildings a hundred yards away from the main colony attracted *Calliphora* spp. most commonly. In the following taxonomic list all species recorded as *adults* on *P. impudicus* by previous authors are given for comparison. The species found by the present author are also included, except those bred, which are dealt with fully below.

The following abbreviations are used, the dates being those on which the actual observations were made, not the year of publication.

C = A. Collart, Belgium, 27th September, 1946.
L = H. Luther, Finland.
P1 = L. Parmenter, England, 3rd October, 1948.
P2 = L. Parmenter, England, 7th November, 1937.
S1 = K. G. V. Smith, England, 31st August, 1954.
S2 = K. G. V. Smith, England, 17th September to 16th November, 1954.

Anisopodidae : *Anisopus fenestralis* Scop. (S2).

Scatopsidae : *Scatopse flavicollis* Mg. (S2), *S. picea* Mg. (S2), *Scatopse* sp. (L).

Mycetophilidae : *Sciara thomae* L. (L), *Sciara* sp. (S2).

Phoridae : *Conicera dauci* Mg. (S2).

Dryomyzidae : *Neuroctena anilis* Fln. (C, P1, S2), *Dryomyza flaveola* F. (P1, P2, S2.).

Sepsidae : one, sp. indet. (S2).

Helomyzidae : *Helomyza affinis* Mg. (C, P2), *H. notata* Mg. var. *hilaris* Zett. (P2), *H. humilis* Mg. (P2), *H. bicolor* Zett. (S2), *H. fuscicornis* Zett. (S2).

Opomyzidae : *Opomyza germinationis* L. (S2).

Sphaeroceridae : *Limosina plumosula* Rond. (L), *Borborus roseri* Rond. (S2).

Asteidae : *Leiomyza scatophagina* Fln. (S2).

Drosophilidae : *Drosophila phalerata* Mg. (S2), *D. subobscura* Coll. (S2), *D. vibrissina* Duda (S2).

Chloropidae ; *Siphonella oscinina* Fln. (L).

Cordiluridae : *Scopeuma lutarium* F. (S2), *S. stercorarium* L. (S2).

Calliphoridae : *Calliphora vomitoria* L. (C, P1, S1, S2,) *C. erythrocephala* Mg. (C, P1, S1, S2), *Cynomyia mortuorum* L. (C), *Lucilia caesar* L. (C), *L. ampullacea* Vill. (P1), *Lucilia* sp. (L, S1, S2) the females taken by the present author were all of the *caesar-ampullacea* complex, *Sarcophaga* sp. (L, S2).

Muscidae : *Hylemyia nigrimana* Mg. (C), *Mydaea depuncta* Fln. (C), *Polietes lardaria* F. (C), *Alloeostylus diaphanus* Wied. (C.), *Phaonia variegata* Mg. (C, P1, P2, S2), *Muscina assimilis* Fln. (C, S2), *M. pascuorum* Mg. (C).

The adult flies visiting the fungus in the present study are given in Tables I–IV. Within each table the species are listed in chronological order of first

Table I.—*Flies visiting " egg " stage fungi.*

	18.ix.	27.ix.	1.x.
Neuroctena anilis	♀	.	.
Helomyza bicolor	♀	.	.
Helomyza fuscicornis	.	♂	.
Helomyza sp.	.	.	♀

TABLE II.—*Flies visiting fruiting body.*

	September.			October.							Nov-ember.
	23	24	29	4	5	13	14	15	16	28	16
Neuroctena anilis	2♂ 6♀	2♂ 5♀	♀	3♀	2♂ 5♀	♀	.	.	.	.	.
Phaonia variegata	♂ ♀	4♀	♂ 4♀	2♀	♂ 18♀	♀	♂ ♀	5♀	♂ ♀	4♂ 5♀	♀
Lucilia sp.	♀	.	♀	.	.	.	.	.	.	.	.
Calliphora vomitoria	*2♀	4♀	8♂ 7♀	.	5♂ 19♀	.	♀	♂	.	4♂ 5♀	♂
Sarcophaga sp.	.	.	47♀	.	47♀	.	.	.	.	2♀	.
Calliphora erythrocephala	.	.	6♂ 18♀	.	11♂ 9♀	2♀	*♀	.	.	♂	.
Dryomyza flaveola	.	.	.	♂	.	.	.	.	♂	.	.
Helomyza bicolor	.	.	.	♂	.	.	.	.	.	♂	.
Scopeuma stercoraria	.	.	.	.	4♀	.	.	.	.	.	.
Drosophila phalerata	.	.	.	.	♂	.	.	.	.	.	.
Scopeuma lutarium	.	.	.	.	♂	.	♂	.	.	.	.
Muscina assimilis	.	.	.	.	♂	.	.	.	.	.	.
Sciara sp.	.	.	.	.	.	.	.	♀	.	.	.
Anisopus fenestralis	.	.	.	.	.	.	.	.	.	.	♀

* Some of these *Calliphora* sp. were dead due to infection with the fungus *Monilia penicillioides* Delacr. (*det.* F. L. Balfour-Browne).

TABLE III.—*Flies found inside broken stem of fungus.*

	24.ix.	27.ix.	29.ix.
Drosophila phalerata	♂ ♀	.	.
Drosophila vibrissina	♀	.	.
Conicera dauci	.	♂	.
Scatopse picea	.	.	♀

TABLE IV.—*Flies on old rotting remains of fungus.*

	17.ix.	27.ix.	30.ix.	5.x.	22.x.
Neuroctena anilis	3♀	.	.	.	.
Opomyza germinationis	.	2♀	.	.	.
Scatopse flavicollis	.	.	♀	.	.
Leiomyza scatophagina	.	.	♂	.	.
Sepsidae (sp. indet.)	.	.	♀	.	.
Dryomyza flaveola	.	.	.	5♂	2♂
Helomyza sp.	.	.	.	♂	.
Drosophila subobscura	.	.	.	♀	.
Drosophila vibrissina	.	.	.	♂	.
Borborus roseri	.	.	.	♂	.
Borboridae (sp. indet.)	.	.	.	♂	.

appearance. Those flies found on *P. impudicus* in the "egg" stage or on rotting remains are species which have previously been bred from other fungi and some of these or related species were bred from *P. impudicus* in the present study.

EFFECT OF SUNLIGHT ON FLY VISITORS.

The main colony of the fungus grew in the shade of a hedgerow and beneath Rhododendrons. Only occasional specimens grew in the open and received a fair amount of sunlight. Such fungi were more frequented by flies. On the morning of 29th September a fruiting body was moved a hundred yards away from the main colony where the shadow of a building provided a convenient opportunity to test the effects of sunlight and shade. To ensure that all flies present were taken, the fungus was placed in a cirular glass trough, four inches deep, so that as the net descended the flies were forced upwards into the net and none escaped at ground level as was often the case when collecting from a growing fungus. During 14 alternate ten minute periods, 24 flies were taken in sunlight, while only 5 were taken in shade. The fly population here differed from that in the main colony in that *Calliphora* spp. predominated. The 29 flies taken were as follows: *Calliphora erythrocephala*, 4 males, 15 females; *C. vomitoria*, 3 males, 3 females; *Sarcophaga* sp., 3 females; *Phaonia variegata*, male.

On the same day, when the sun was in a suitable position, a similar test was made within three yards of the main colony, with more striking results. This time the fungus was placed in sunlight and shade for alternate periods of five minutes and although in the shade position the fungus was only two feet away from the sunlight position, no flies were attracted. In three five minute periods in sunlight 61 flies were taken as follows: *Phaonia variegata*, 4 females; *Neuroctena anilis*, female; *Calliphora erythrocephala*, male, 2 females; *C. vomitoria*, 4 males, 4 females; *Sarcophaga* sp., 44 females; *Lucilia* sp. female.

These results show that sunlight plays a large part in governing the activity of these, normally carrion-feeding flies, as has also been shown by Green (1951) in his studies of species infesting slaughter houses.

Flies Bred from the Fungus.

The technique adopted was to remove each fruiting body as soon as it ceased to attract flies, though a few were left to rot a little first so that all stages of attractiveness to ovipositing females were covered. The remains were kept in very fine muslin-covered glass cylinders in the laboratory and examined at frequent intervals for developing larvae, samples of which were preserved.

TIPULIDAE.

Ula sylvatica Meigen.

Several larvae were found in the fungus from which a female was bred on 16th October, 1954. Edwards (1938 : 62) states that this common species breeds in fungi; Coe (1941 : 172) records it from *Pholiota spectabilis* (Weimann) Kumner; Niblett (1955 : 151) has bred it from *Lactarius vellereus* (Fr.) Fr. (both AGARICALES).

CECIDOMYIIDAE.

Lestremiinae.

One small red Cecidomyiid larva was found in the stem of a fruiting body examined on 25th September, 1954. Dr. H. F. Barnes has kindly examined it and informs me (*in. litt.*) that it belongs to the subfamily Lestremiinae. The specimen is now in Dr. Barnes' collection (slide no. 10,000). In the hope that some future worker will establish the identity of this midge, I have figured the " anchor " process (fig. 1.).

Miss J. A. T. Anderson (1936) records 28 described species and over 50 undescribed species of world Cecidomyiidae associated with fungi. Most of these are *Mycodiplosis* spp. and other Cecidomyiinae, but six species are Lestremiinae, two from mushrooms, two from moulds and one from the fungus-affected heartwood of a hard pine. Prof. P. A. Buxton and Dr. H. F. Barnes (1953 : 195) give three further species of Lestremiinae, all reared from cultivated mushrooms. Buxton (1954 : 168) gives a further record from young sporangia of the Myxomycete *Arcyria incarnata* (Pers.) Pers.

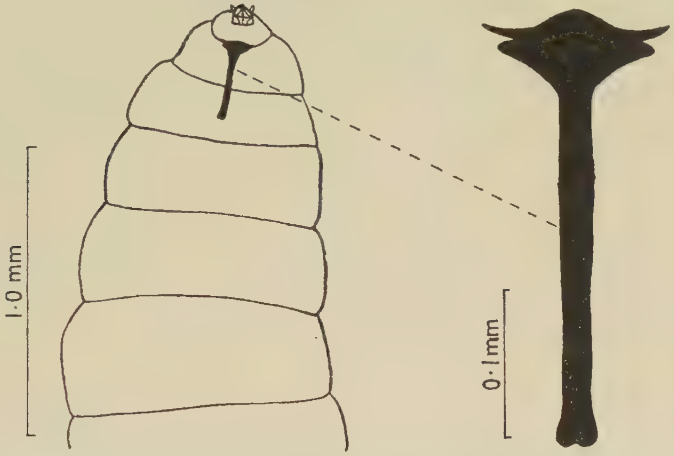

Fig. 1.—"Anchor" process of gall midge larva (Lestremiinae) found in stem of *Phallus impudicus* Pers.

PHORIDAE.

Megaselia rufipes Meigen.

Many larvae were noted and about 20 pupated successfully. Some dozen adults emerged 24th–27th January, 1955. Colyer (1954) summarises the known breeding media of this species, which has previously been bred from fungi, though not from *P. impudicus*.

SPHAEROCERIDAE (BORBORIDAE).

Leptocera parapusio Dahl.

One female was bred 11th October, 1954. Prof. O. W. Richards informs me that this species is known to breed in fungi and in his paper (1930 : 303) records it as more rarely found on carrion or in rabbit burrows.

DROSOPHILIDAE.

Drosophila busckii Coquillett.

Drosophila eggs were found quite commonly on the growing " egg " stage fungus. All bred were *D. busckii* Coq., though several other species were seen as adults on the later stage fungi. *D. busckii* eggs hatched on 1st October, 1954 and adults emerged from 11th to 19th October, 1954.

Basden (1952 : 200) says that *D. busckii* prefers decaying rather than fermenting substances as a breeding medium. From the egg laying habits described above it would appear that the eggs do not hatch until the fungus has fruited and is in an advanced state of decay. Though this seems unlikely, it would certainly explain why larvae were not detected in the fruiting body, although eggs had been found commonly on the " egg " stage fungus, and larvae in the rotting remains of old fungi.

OTHER INSECTS AND INVERTEBRATES ASSOCIATED WITH THE FUNGUS.

THYSANOPTERA.

One fruiting body was found to be infested with Thysanoptera (*vide* Smith, 1955*b*). Dr. G. D. Morison has kindly identified the following species : THRIPIDAE : *Taeniothrips atratus* Hal., *T. vulgatissimus* Hal., *Thrips flavus* Schrk., *T. fuscipennis* Hal., *T. major* Uzel.

LEPIDOPTERA.

At dusk on the evening of 16th November, 1954, a male *Conistra vaccinii* L. (CARADRINIDAE) was netted on the fungus. It would be interesting to explore the value of this fungus as a source of attraction to nocturnal Lepidoptera and other insects. Luther (1946) records *Phytometra gamma* L. as visiting the fungus in Finland, though presumably this was in daytime.

COLEOPTERA.

The following beetles, kindly identified by Mr. P. J. Osborne, were found *in* the fungus, usually in the base, at or just below soil level.

STAPHYLINIDAE : *Proteinus ovalis* Steph., *Omalium rivulare* Payk.

NITIDULIDAE : *Epuraea aestiva* L.

MYCETOPHAGIDAE : *Mycetophagus quadripustulatus* L.

Luther (1946) records the following Coleoptera from Finland :—

CARABIDAE : *Feronia* (*Pterostichus*) *nigra* Schall., *F. vulgaris* L.

SILPHIDAE : *Necrophorus vespilloides* Hbst., *Oeceoptoma thoracicum* L., *Silpha carinata* Hbst. (larva).

CERAMBYCIDAE : *Strangalia quadrifasciata* L.

HYMENOPTERA.

Vespula spp. were attracted and hovered around the fungus when the fruiting body was ripe, but none were seen to settle. Flies immediately vacated the fungus when a wasp approached.

MOLLUSCA.

Luther (1946) records the slugs *Limax cinereoniger* Wolf and *Arion subfuscus* Férussac in Finland ; Ramsbottom (1953 : 180) gives *Limax maximus* L. as the slug usually found feeding on the fungus. A specimen of *Arion ater* Gray was the only slug found in the present study though other species were probably present as the area was covered with snail tracks and there was much evidence of feeding.

ACKNOWLEDGMENTS.

I am indebted to the late Prof. P. A. Buxton, Prof. G. C. Varley and Dr. B. M. Hobby for kindly reading the manuscript and for useful criticism. Thanks are also offered to the following specialists for determinations in their respective groups : Mrs. F. L. Balfour-Browne, Mr. R. L. Coe, Mr. C. N. Colyer, Dr. G. D. Morison, Mr. P. J. Osborne and Prof. O. W. Richards.

Dr. A. Collart, Mr. E. B. Basden and Mr. M. Niblett are thanked for kindly sending copies of their papers. Mr. H. M. Parker kindly told me of the colony of *P. impudicus* on which this study is based.

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OBSERVATIONS ON THE BEHAVIOUR AND MORTALITY IN COCCINELLIDAE BEFORE DISPERSAL FROM THE EGG SHELLS.

By C. J. Banks, Ph.D., F.R.E.S.

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When ladybird beetles are numerous on bean plots and have laid many egg batches, cannibalism may be an important cause of mortality of the immature stages; larvae dispersing from the eggs in search of food encounter and eat unhatched eggs and newly-hatched larvae clinging to the egg-shells before they are old enough to disperse (Banks, 1955).

Even when coccinellid populations are low there is a certain degree of mortality during the egg stage, for some eggs are apparently infertile and some unhatched larvae may be destroyed by larvae already hatched from the same batch. Hawkes (1920) observed that some eggs of *Adalia* 2-*punctata* hatched earlier than others and that approximately a quarter of the larvae were eaten before dispersal. Smee (1922) also noted that newly-emerged larvae attacked unhatched eggs and that some eggs were infertile. Jöhnssen (1930) recorded that, on the average, 40 per cent. of the eggs of 9 batches of *Coccinella* 7-*punctata* and only 6 per cent. of eggs of 9 batches of *A.* 2-*punctata* did not hatch, but he did not express the mortality as infertile eggs and those in which larvae had developed. He noted that larvae after hatching frequently ate the empty egg-shells, infertile eggs and larvae which for some reason did not emerge.

The mortality in the egg stage in Coccinellidae is discussed here with reference to three common species of bean plots, *Coccinella* 7-*punctata* L., *Adalia* 2-*punctata* (L.), and *Propylea* 14-*punctata* (L.).

Hatching.

In all three species hatching takes place approximately seven days after oviposition. The eggs remain yellow until a few hours before eclosion, when they darken and the eyes of the larva show through the chorion. Infertile eggs do not darken and cannot be distinguished, unless damaged, until the hatching of fertile eggs is well-advanced. The larva emerges through an apical split in the chorion and the pronotal egg bursters assist in hatching (van Emden, 1949). The head, thorax and legs are gradually drawn free of the embryonic cuticle and chorion by slow backward and forward movements, and the larva rests on top of the egg-shell with part of the abdomen remaining inside. In this position it remains for an hour or so while the cuticle darkens and hardens.

After a while, the insect makes small movements, sometimes withdrawing the abdomen entirely from the chorion; it may crawl over its fellows and unhatched eggs; more usually it crawls out of the shell, retaining a hold at the top with the tip of the abdomen (the evaginated rectum acts as a sucking disc which is used in locomotion (Gage, 1920)) and brings its head to the base of the shell. Small movements of the head and the presence of small holes in the base of the thin-walled chorion suggest that the larva sucks out any fluid remaining within the shell. Empty egg-shells may be completely eaten before larvae disperse.

Larvae remain on or near the empty egg-shells for 12–24 hours or more after eclosion (" just-hatched " stage) (Plate 1B) and it is during this time that the destruction of infertile eggs and larvae slow in hatching occurs.

SIZE OF EGG BATCHES AND RATES OF MORTALITY.

The number of eggs per batch in *P.* 14-*punctata* is usually 6 or 7, although as many as 11 have been seen. In *A.* 2-*punctata* the number is variable, the average being between 12 and 17 ; a maximum of 36 eggs in a batch has been recorded in this species. In *C.* 7-*punctata* the number of eggs is also very variable and, although there are usually 20 to 30 eggs, large batches of 40 to 50 eggs are not uncommon, and in one batch 65 eggs were recorded. Smee (1922) gives averages similar to these.

When there are few eggs in a batch the larvae usually emerge together and any attack on one larva by another is usually repulsed. But in larger batches hatching may be spread over a longer time and thus some larvae hatch earlier than others and will attack unhatched eggs and even larvae partly emerged. Thus, the hatching of a batch of 53 eggs of *C.* 7-*punctata* on 6th June was spread over seven hours. During the first three hours only 6 larvae emerged, but 11 more hatched during the next 25 minutes and were followed by 9, 10, and 9 larvae in successive intervals of 30 minutes ; the hatching of 45 eggs lasted four and a half hours (fig. 1). There was a general but not very marked tendency for eggs which had been laid first to hatch early and, in this example, the four infertile eggs and one unhatched larva were destroyed by cannibals.

Infertile eggs are always attacked, sometimes by more than one larva, and the contents sucked out ; their remains can be recognised by their shrivelled appearance and by traces of yellow yolk. Eggs which would have hatched but for an attack are also collapsed, but the dark remains of larvae within the shells distinguish them from infertile eggs.

In *P.* 14-*punctata*, where the egg batches contain few eggs, nearly all larvae hatch together and the proportion of fertile eggs destroyed by cannibals is low (about 6 per cent.) ; in *A.* 2-*punctata* and *C.* 7-*punctata* where batches are larger this proportion is considerably higher (10–12 per cent.) (Table I).

TABLE I.—*Mortality of Coccinellidae in the egg stage.*

	C. 7-*punctata.*	*A.* 2-*punctata.*	*P.* 14-*punctata.*
Number of batches . . .	16	11	10
Number of eggs	499	186	57
Mean eggs per batch . . .	32	17	6
Proportion of infertile eggs (%) .	13·2	4·8	5·3
Proportion of fertile eggs eaten by larvae already hatched (%) .	9·5	12·4	5·6
Proportion of total eggs from which no larvae were obtained (%) .	21·4	16·6	10·6

Infertile eggs are uncommon in *P.* 14-*punctata* and *A.* 2-*punctata*, but in *C.* 7-*punctata* they occur regularly and are invariably eaten by the larvae before they disperse.

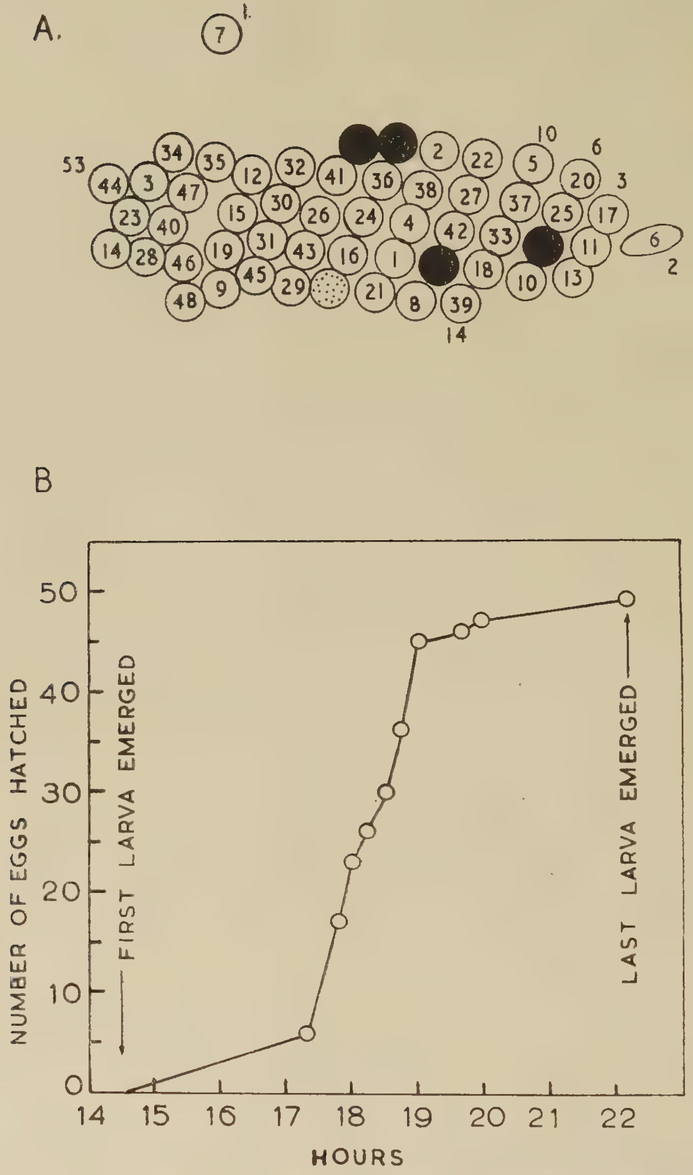

Fig. 1.—Hatching of a batch of 53 eggs of *Coccinella 7-punctata*. A. Plan of the batch; the numbers within the eggs show the order of hatching, those outside, the order in which they were laid. The infertile eggs (in black) and one fertile egg (stippled) were eaten by larvae. B. The numbers of eggs hatched over a period of 8 hours.

Larvae which have eaten a coccinellid egg are easily recognised by the distended abdomen, and the separation of the thoracic and abdominal segments shows the yellow contents of the gut through the integument (Plate 1A).

Five newly-hatched larvae of *A.* 2-*punctata* were fed on one egg each of their own species ; on the average they lived almost twice as long as unfed larvae (fig. 2). Other larvae of the same age, provided with two and three eggs but no other food, lived still longer and reached the second instar within four days after hatching, the usual time for this species when abundant aphids are provided (4·6 days, Clausen, 1916 ; 4 days, Smee *loc. cit.*). Water extended the life of unfed larvae by only a few hours.

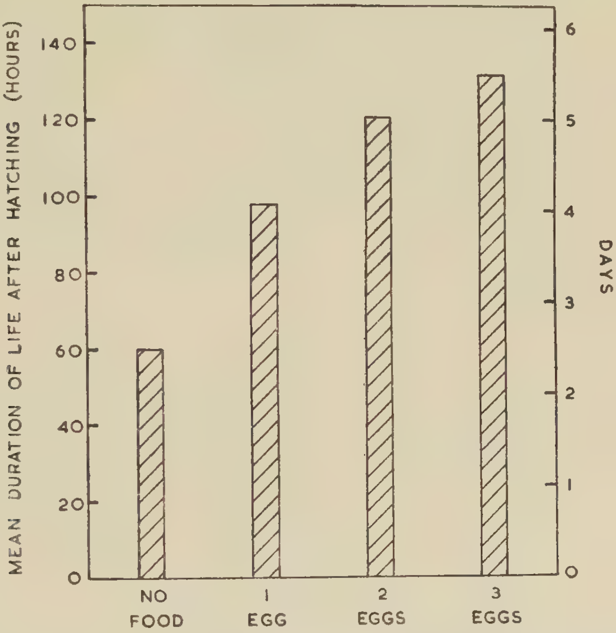

FIG. 2.—The average duration of life of 4 groups of 5 newly-hatched larvae of *Adalia 2-punctata*. One group had no food ; the 5 larvae of the other groups were fed on 1, 2 and 3 eggs of this species.

If this early cannibalism before dispersal occurs in the field, and there is no reason to suppose that it does not, then larvae which hatch early and are able to eat an egg probably benefit in that by living longer they are able to make a more prolonged search for aphids. When prey density is low cannibalism would have a survival value for individual larvae. The numbers of larvae which would benefit in this way is, however, unknown, and all that can be said at present is that the numbers would apparently be correlated with the size of the egg batch and, therefore, with the species, that is, lower in *P.* 14-*punctata* than in *A.* 2-*punctata* and highest in *C.* 7-*punctata.*

ACKNOWLEDGMENT.

I am indebted to Mr. V. Stansfield for the photographs.

SUMMARY.

In the three common species of Coccinellidae occurring on bean plots, *Coccinella 7-punctata*, *Adalia 2-punctata* and *Propylea 14-punctata*, important causes of mortality in the egg stage were infertility and predation by newly-hatched larvae of the same batch.

The extent of this predation appears to be associated with the size of the egg batch ; in *C. 7-punctata* and *A. 2-punctata*, which have large or medium-sized egg batches, 10–12 per cent. of the fertile eggs were destroyed by larvae already hatched and in *P. 14-punctata*, where egg batches are small and the larvae usually hatch together, approximately 6 per cent. of the fertile eggs were destroyed in this way.

Infertile eggs were not common in *A. 2-punctata* and *P. 14-punctata*, but in *C. 7-punctata* they occurred regularly and were always eaten by the young larvae.

The advantage to larvae which are able to eat an egg before starting a search for prey is emphasised by the results of an experiment which indicated that the provision of one cocinellid egg as food almost doubled the life of a newly-hatched larva, which would thus be able to prolong its search for aphids. Larvae fed on two and three eggs lived even longer and were able to grow into second instars without aphid food.

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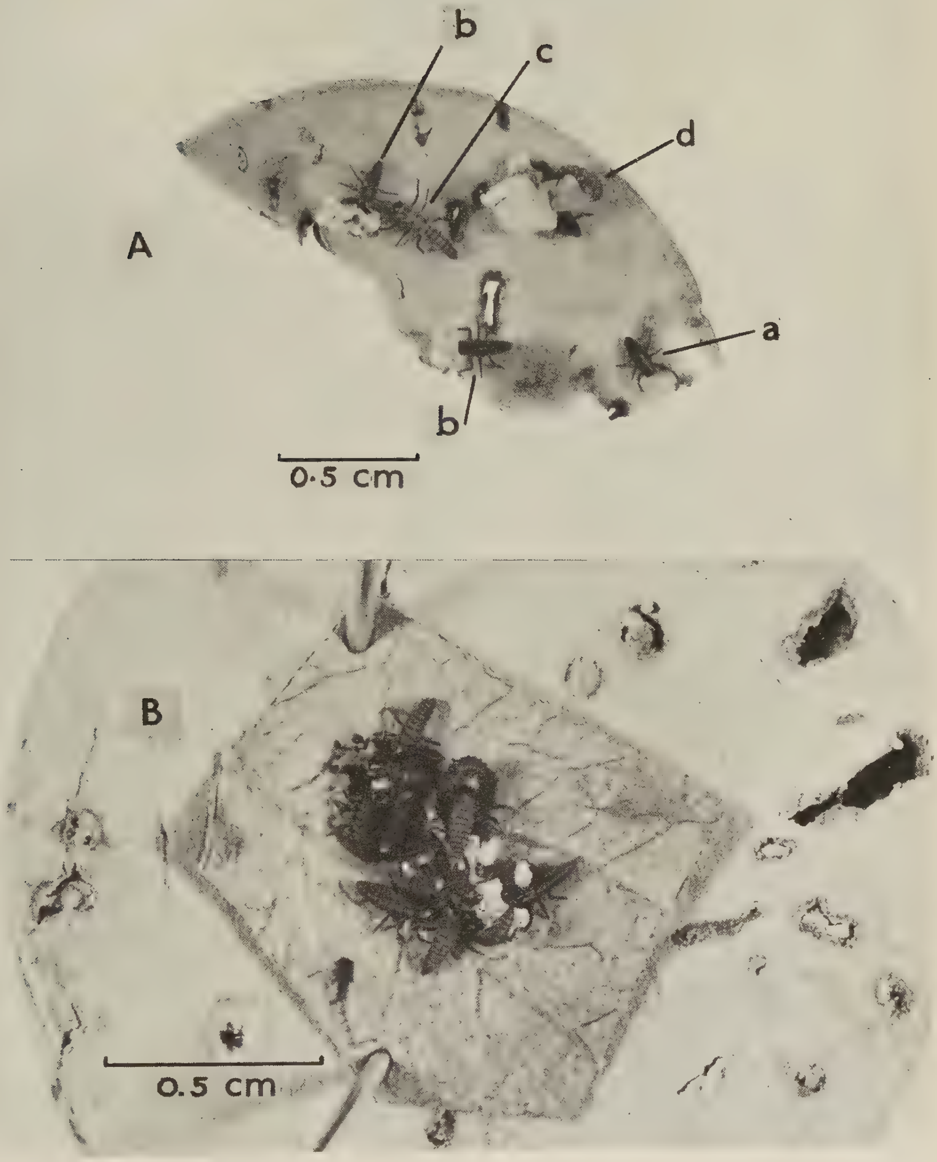

A. Newly-hatched larvae of *Propylea* 14-*punctata* on a piece of cork. (*a*) unfed larva; (*b*) unfed larvae attacking eggs; (*c*) fed larva showing distended abdomen; (*d*) egg collapsing under attack by larva.

B. " Just-hatched " larvae of *Adalia* 2-*punctata* on the undersurface of a piece of rose leaf.

C. J. Banks.

Adlard & Son, Ltd, Dorking.

BENEFICIAL EFFECTS OF THE COMMON GARDEN ANT, *LASIUS NIGER* L., ON THE BLACK BEAN APHID, *APHIS FABAE* SCOPOLI.

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Reviewing the literature, Nixon (1951) cites a number of cases where the association between ants and aphids appeared to benefit not only the ants, but also the aphids. The ant-attended aphid colonies grew faster than unattended colonies, as well as giving a healthier impression because free of honey-dew, moulds and exuviae. As to how the ants exert their beneficial effects on the growth of the aphid colonies, the evidence refers almost entirely to defence of the aphids against attacks by their natural enemies, and Nixon concluded that the amount of such protection afforded by ants has been much exaggerated. But a second and more directly beneficial effect was suggested by Herzig's (1937) circumstantial evidence that ant-attended individuals of *Aphis fabae* Scopoli and *A. sambuci* L. fed faster than unattended ones.

The following observations were made in the grounds of the Entomological Field Station, Cambridge, in 1954 and 1956. The procedure throughout was to set up " standard " colonies of laboratory-bred aphids within reach of free-living ants. The aphid colonies were started by transferring similar numbers of adult apterous virginoparae from the mass culture described by Kennedy and Booth (1954), to similar, 1 ft.-high, growing plants of *Vicia faba* var. Seville Longpod in pots, and leaving the aphids in the dark overnight to settle down before exposing them.

1. Effects of Ant-attendance upon Aphid Colonies Exposed to Enemy Attack.

When four " standard " aphid colonies were set out in the middle of a large stubble field, the colonies remained free of ants. Very few natural enemies were seen on or near these plants at daily inspections, but a single coccinellid adult was seen activily feeding on one or other of the colonies on several occasions ; and the colonies grew very slowly. Two other lots of four pot colonies each were set up at the same time, one in the middle of an open plot in the garden and the other close to the hedge. Both lots were quickly and regularly attended by ants. Although parasites and predators were constantly seen near-by, none was ever noticed attacking the aphids, and the colonies grew rapidly without producing as many winged forms as the colonies on the open field. In order to check whether the ants were mainly responsible for this difference between the colonies in different situations, six pot colonies were set up near the hedge, every alternate one surrounded by an oil tray which effectively denied the ants access to the plant, while the other three colonies were left accessible to and regularly attended by the ants.

After three weeks the ant-attended colonies were large, densely aggregated and lightly parasitised, whereas the isolated colonies were still small, dispersed over the plants and heavily parasitised. The ant-attended colonies were also perfectly clean, whereas the isolated plants were littered with exuviae and honey-dew upon which moulds were growing. Table I shows the difference in total aphid numbers at this time, and also shows a striking difference in the proportion of winged forms present. The visibly winged forms constituted the majority of the aphids in the ant-free colonies, but only a minority on the ant-attended colonies in spite of the much higher aphid density there. Eventually, as was to be expected, the ant-attended colonies also produced winged forms *en masse*, but not until they had grown substantially larger and denser than at the time of the above counts.

TABLE I.—*Effect of ant-attendance on the size and composition of exposed aphid colonies.*

	Ant-attended colonies		Ant-free colonies.	
Plant.	Total aphids.	% alates.*	Total aphids.	% alates.*
A . . .	1486	13	450	61
B . . .	1946	17	208	57
C . . .	1555	17	378	65

* Third and fourth instar nymphs, as well as adults.

2. PROTECTIVE ACTIVITIES OF THE ANTS.

Various natural enemies of the aphids were collected alive and installed in aphid colonies during the temporary absence of ants, in order to observe the reactions of the ants when they returned and encountered these intruders. The approximate numbers of individual enemies used in these tests were as follows: *Adalia bipunctata* (L.) larvae, second instar—9, full-grown—20; syrphid larvae—15; coccinellid adults: *A. bipunctata*—10, *Coccinella septempunctata* L.—5, *Propylea quatordecimpunctata* (L.)—2; *Aphidius* sp. adult females—12. In addition, 30 coccinellid eggs and 4 syrphid eggs were placed close to aphid colonies. These did not seem to evoke any response from the ants. Soon after they had hatched, however, the young larvae had disappeared.

When the second-instar coccinellid larvae that had been installed in the aphid colonies had settled down to feed there, and the ants encountered them in the course of their palpation of successive aphids, the following sequence of events was observed. Instead of palpating the larva once and then moving on, as the ants did with aphids which produced no honey-dew droplet on that occasion, the ant palpated ("solicited") the larva again, and then attacked it with its jaws. The larva at once secreted drops of yellow fluid from the repugnatorial glands on its abdomen, smearing the ant's head and causing the ant to move about jerkily while wiping its head on the leaf surface. The ant returned to the attack, and eventually picked up the larva in its mandibles, ran to the edge of the leaf and dropped the larva off the plant. All the small larvae were disposed of in this way. The larger coccinellid larvae were not picked up bodily (presumably because too heavy) but were repeatedly attacked and gradually driven away, usually off the plant altogether. The syrphid larvae, also, were attacked after palpation, and defended themselves with a repellent fluid but were finally carried or driven off in much the same way. The adult coccinellids were attacked apparently on sight, before palpation, and driven off by persistent biting and harrying. The *Aphidius* adults did not so readily elicit attack, but were often driven off by an ant apparently running at them. It may be added that on six occasions encounters between ants and coccinellids were observed on the rims of the pots containing the bean plants. The ants were on their way to or from the aphid colonies on the plants, but on the pot rims they reacted to the coccinellids as they did to each other—briefly palpating but then continuing on their way without attacking.

These few observations showed that the ants would actively repel freshly-installed enemies of the aphids they were attending, but left open the questions as to how efficient this protection might be over a period, and how far it might account for the faster multiplication and smaller proportion of winged forms in the aphid colonies attended. This last question was considered in the next experiment.

3. Independent Effects of Ants and Natural Enemies.

Six of the standard pot colonies were set up near the hedge, each plant being fitted with a muslin cover on a cylindrical wire frame. On two plants the cover was closed tightly round the pot against the entry of both ants and natural enemies. On two other plants the cover was also closed tightly against ants, but, before that was done, two third instar larvae of *Adalia bipunctata*, one syrphid larva and two freshly-emerged *Aphidius* adults were released inside the cover. On the two other plants the cover was left loosely open at the bottom to admit ants, but no enemies were introduced and none was seen inside at daily inspections thereafter, when ants were seen in regular attendance upon the aphids.

The aphid counts taken after twelve days are shown in Table II, where "alate" again refers to third and fourth instar nymphs as well as adults, and "apterous nymphs" refers to all nymphs not visibly alate, i.e. truly apterous third and fourth instar together with first and second instar nymphs of either form. The figures in the Table are means for the two plants of each kind.

Table II.—*Independent effects of ants and of natural enemies on the size and composition of aphid colonies.*

Colonies accessible to:	Total aphids.	Adult apterae.	Apterous nymphs.	Per cent alates out of total.
Ants only . . .	384	256	94	8·9
Enemies only .	209	68	4	65·6
Neither . .	277	129	9	50·2

It is apparent that the growth of the aphid colonies had been somewhat reduced by the enemies alone in the absence of ants (compare lines 2 and 3 in Table II); but at the same time colony growth had been substantially increased by the ants alone in the absence of enemies (compare lines 1 and 3). The ants thus benefitted the aphids directly, quite apart from any indirect benefit they may sometimes confer by holding the aphids' enemies at bay.

With the short period allowed for colony growth in this experiment, the counts of total aphids do not provide as good an indication of the trend of events as the counts of adult apterae (the first generation produced on the plants), on which the future growth of the colony would depend. It was in this respect that the effect of the enemies was most marked (Table II), for the colonies isolated from both ants and enemies contained twice as many adult apterae as the colonies with enemies. Yet the ant-attended, enemy-free colonies contained twice as many adult apterae again, together with many apterous nymphs which were rare in both types of ant-free colony.

Associated with this higher rate of multiplication in the ant-attended colonies, was the small minority of alate forms produced there despite the greater density of the aphids. Alate forms constituted over half the population on the ant-free plants, whether enemies were present or not. The ants were apparently exerting some control over the physiological mechanism of form-determination in the aphids, keeping them in the more fecund, more sessile, apterous form. The simplest suggestion as to the manner of this control might be that the ant raises the plane of nutrition of the aphid, perhaps as a result of stimulating its excretion and thereby its feeding as Herzig (1937) thought.

The direct influence of the ants was checked later in a glasshouse where *Lasius niger* was found active in April in the complete absence of natural enemies of aphids. The ants were daily carrying off large numbers of caterpillars of *Pieris brassicae* L. from nearby potted cabbage plants, but were never seen carrying aphids. Ten fresh apterae from the laboratory culture of *A. fabae* were placed on each of twelve broad bean plants growing in pots, all 8 in. high and with five expanded leaves. Six of the plants were left accessible to the ants which attended the aphids on them assiduously, while alongside them the other six plants were isolated in an oil tray. The first F_1 adults appeared after 11 days when the colonies on the ant-attended plants were already noticeably larger and denser than those on the ant-free plants. The new adult apterae and alatae wandered, as is their habit, over and off the plants, and about three times as many adult apterae were counted wandering from the ant-attended as from the ant-free colonies whenever they were examined during the next several days. The ants did not appear to interfere at all in this movement. Many of the aphids produced on the plants had therefore departed, especially from the ant-attended colonies, before the counts shown in Table III were made on the 14th day. Nevertheless the figures (in the same categories as before) confirmed in every way the previous findings outdoors.

TABLE III.—*Effect of ants alone on the size and composition of aphid colonies : means and standard errors from six plants under each treatment.*

	Total aphids.	Adult apterae.	Apterous nymphs.	Per cent alates out of total.
Ant-attended .	220±20	44±5	173±22	1±0·3
Ant-free . .	133±13	24±3	53±14	46±7

As far as these preliminary observations go, it thus appears that the association between *Lasius niger* and *Aphis fabae* is a truly symbiotic one, in that both partners gain from it nutritionally ; the protective activities of the ants being perhaps a secondary matter.

SUMMARY.

In field experiments with colonies of *Aphis fabae* attended by *Lasius niger* the ants afforded some protection to the aphids against their natural enemies; at the same time, whether enemies were present or not, the ants increased the rate of aphid multiplication and delayed the production of winged forms. These direct effects were confirmed in a glasshouse experiment.

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LARVAE OF SOME FURTHER EAST AFRICAN TRICHOPTERA.

By N. E. Hickin, Ph.D., F.R.E.S.

The methods of collecting and rearing and the collecting stations in Uganda are described in a previous paper (1955, *Proc. R. ent. Soc. Lond.* (A) **30** : 155–163). I am indebted to Mr. D. E. Kimmins for identification of the reared adults. The species the larvae of which are described below belong to the Leptoceridae—a family well represented in East Africa.

Leptoceridae.

Leptocerina ramosa pinheyi Kimmins.

A number of larvae subsequently determined as this species was collected from a stream at Namugongo on 8th May and 4th June, 1954, and at Sezibwa Falls on 25th May, 1954. These larvae gave rise to adults on 21st and 25th May, 1954, at Jinja and on 3rd July, 1954, in an aquarium at Bletchingley, Surrey, England.

Case (fig. 1) of three similarly shaped pieces of cut leaf, arranged to give triangular cross-section, each piece hastate with obtuse end anterior. In the aquarium a number of different types of leaf were observed to have the characteristically-shaped pieces cut from their edges (fig. 2). Length 17·0 mm., width 2·5 mm. *Larva* swims well by rapid beats of metathoracic legs. The green cases were several times observed moving rapidly near the surface of the dark-coloured water both at Namugongo and Sezibwa Falls and made these the most conspicuous Caddis larvae I have ever observed. Length 10·0 mm., width 2·0 mm. Pro-and meso-nota sclerotised. *Head*, pro- and meso-nota dark brown with lighter markings, *metathorax* and *abdomen* light yellow, inter-segmental grooves well developed, median dark longitudinal line along abdomen. Pro- and meso-nota (fig. 5) approximately as wide as head but metathorax and abdomen at least twice as wide as head. *Antennae :* proximal segment bulbous, white with dark encircling band, distal segment long, dark grey with long terminal bristle. *Labrum* golden brown, lateral margins heavily sclerotised, chestnut brown. Lateral bristles long. *Mandibles* asymmetric, left mandible larger than right and extending farther forwards. *Maxilla* with four blade-shaped bristles. Maxillary palp four-segmented.

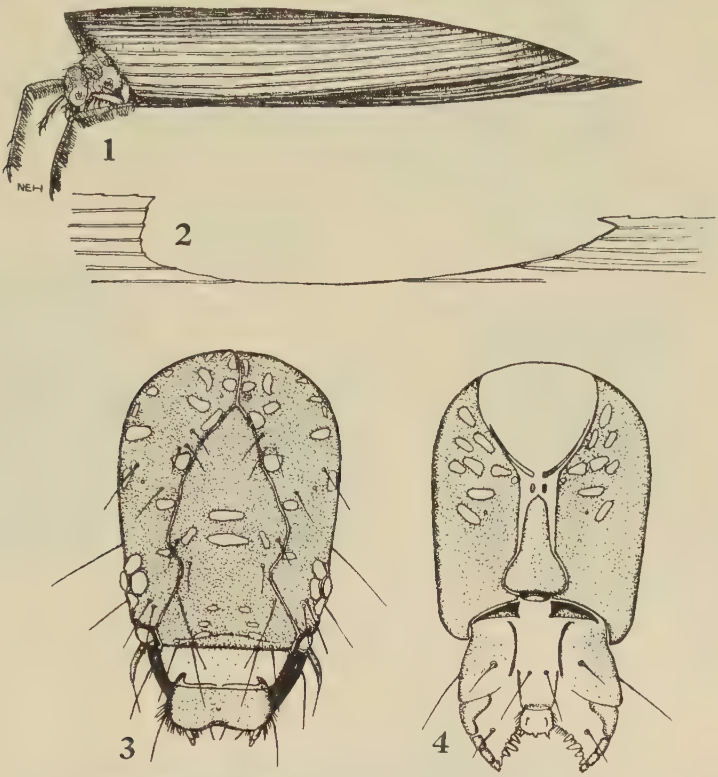
Leptocerina ramosa trifida Kimmins.

Larvae of this species were collected at the Namugongo stream on 8th and 25th May, 1954. From these three adults emerged as follows : one female (12th July, 1954) at Jinja, and a female (16th July) and a male (18th July) at Bletchingley, Surrey. This larva swims well with its large case after the fashion of other species in this genus.

Case (fig. 8) of vegetable debris, etc., pieces from 2–5 mm. in length, arranged transversely (somewhat reminiscent of the case of *Limnephilus rhombicus* L. of Europe) but usually one or two pieces rather longer (about 10 mm.). Length of case 20 mm., width 6 mm., posterior end sometimes quite narrow. *Larva :* length 11·0 mm., width 2·5 mm.

PROC. R. ENT. SOC. LOND. (A) 31. PTS. 4–6. (JUNE, 1956).

Abdomen creamy-yellow, uniformly cylindrical. Larva is like that of *L. ramosa pinheyi* Kimmins, but may be distinguished from that sub-species and from *L. ugandana* (Ulmer) by the almost complete black coloration of the head, pro- and mesonota. The " muscle-spots ", however, are light in colour and show up quite clearly, as in figs. 9 and 10. Eyes situated in light areas (visible to the naked eye). Lateral margins of gular sclerite only just perceptibly concave, whilst in *L. ramosa pinheyi* they are much more concave. In *L. ugandana* the lateral margins are definitely concave and the aboral apex is somewhat dilated. The black-banded mesothoracic legs of *L. ramosa trifida* Kimmins are characteristic (fig. 12). Protuberances (dorsal and lateral) on first abdominal segment bulbous and prominent. Long single filiform gills present. Anal sclerite not defined. Three large and two small black bristles arise from each side of a yellowish but apparently membraneous area.

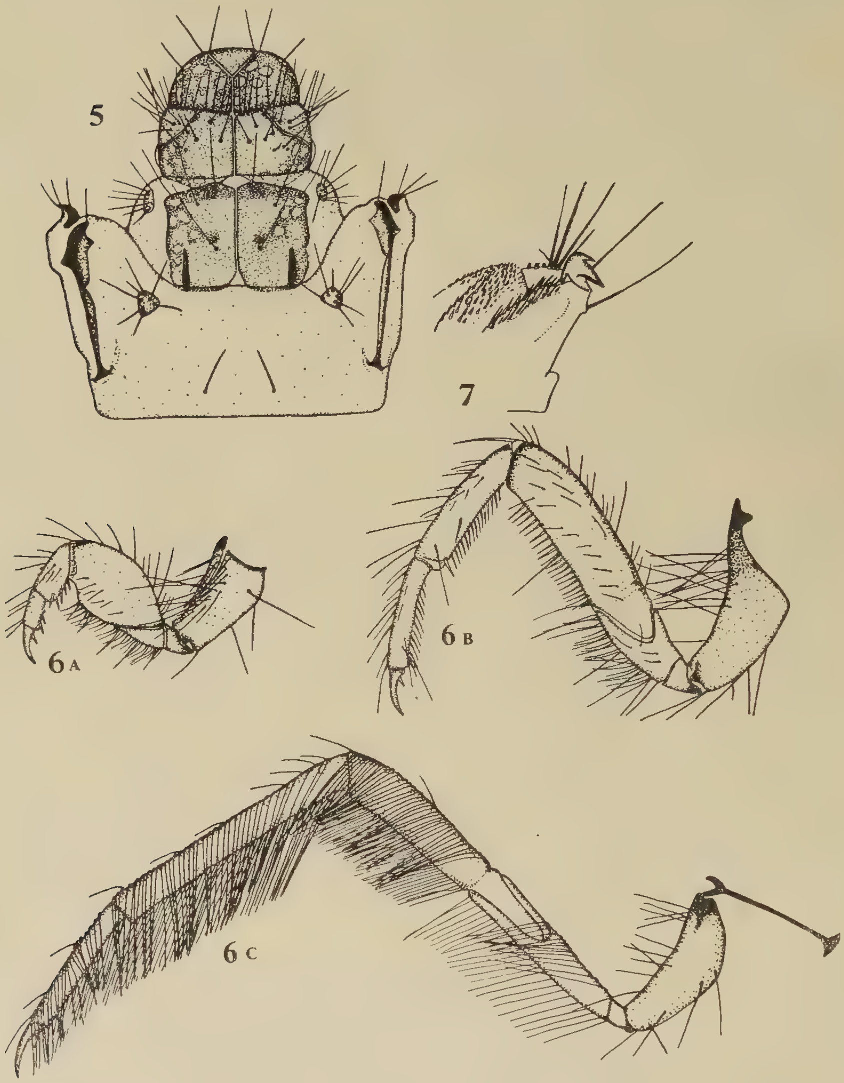


Figs. 1–4.—*Leptocerina ramosa pinheyi* Kimmins. (1) Larva in case. (2) Edge of leaf from which segment has been cut by larva. (3) Head from the front. (4) Head from below.

Leptocerina ugandana (Ulmer).

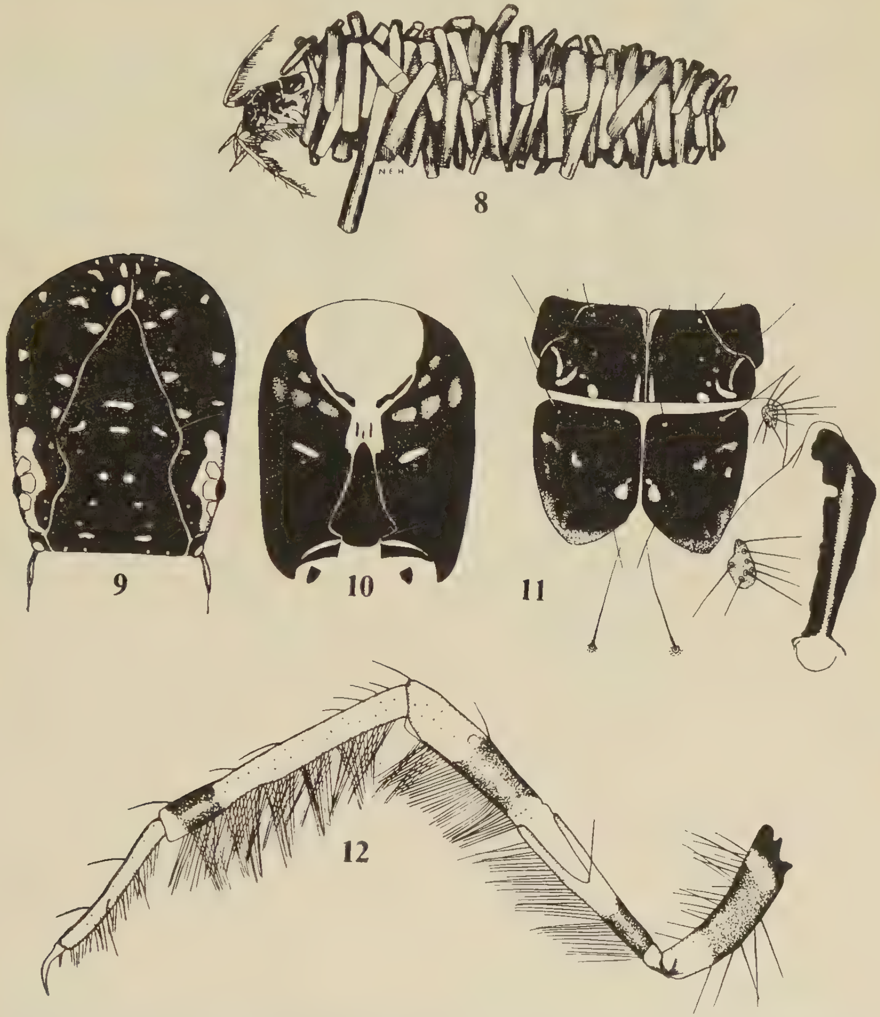
Ulmer's description of the adult of this species is under the name *Leptocerus ugandanus*. Larvae of this species were collected on 8th May and 4th June, 1954, at the Namugongo stream. Adults emerged on 8th June, 1954, in an aquarium at Jinja.

Case (fig. 13) usually a single piece of twig or stalk hollowed out wholly or in part by the larva. A few small pieces of vegetable debris may be added at one end. Larvae in the aquarium readily accepted pieces of wheat straw 25 mm. in length and inhabited them.

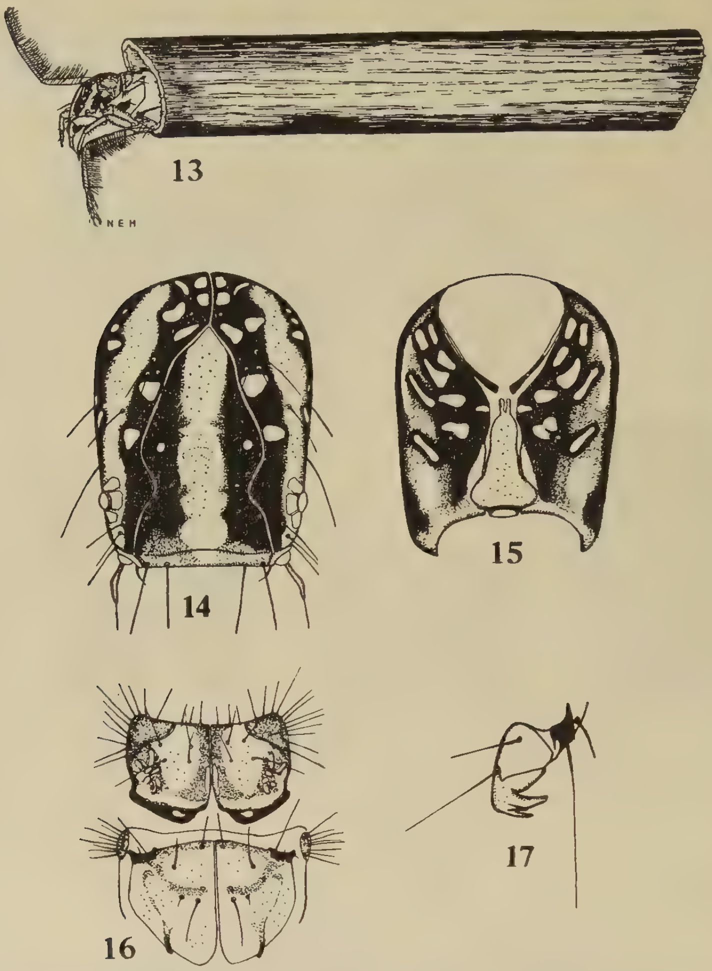


Figs. 5–7.—*Leptocerina ramosa pinheyi* Kimmins. (5) Thoracic nota. (6) (*a*) Prothoracic leg; (*b*) mesothoracic leg; (*c*) metathoracic leg. (7) Anal claw with basal segment from beneath.

Larva swims well, taking its case with it and seems to spend much time swimming. Length 14·0 mm., width 2·25 mm. *Abdomen* creamish to yellowish-orange. Larva very like *Leptocerina ramosa pinheyi* Kimmins in shape but may be readily distinguished from it as follows: *Head* (fig. 14 and 15) yellowish with very dark, almost black, longitudinal bands stretching from cervical margin of genae to oral margin of clypeus. Inner edges of the bands extend within the clypeus, but a pronounced yellowish longitudinal band stretches from aboral angle of clypeus to oral margin. " Muscle spots " light in colour and well marked. Gular sclerite slightly dilated at its aboral end, and the contiguous areas of the genae black, the " muscle-spots ", however, being well-marked. *Pronotum* (fig. 16): A longitudinal dark area extends on each side of the suture and four bristles are present in each heart-shaped light area. Anterior-lateral areas cut off by the diagonal sutures dark in colour. Sclerotised plate forming the mesonotum bears a transverse saddle-shaped mark with a spur-like part extending to the posterior margin.



FIGS. 8–12.—*Leptocerina ramosa trifida* Kimmins. (8) Larva in case. (9) Head from the front. (10) Head from beneath. (11) Thoracic nota. (12) Metathoracic (swimming) leg.



Figs. 13–17.—*Leptocerina ugandana* (Ulmer). (13) Larva in case. (14) Head from the front. (15) Head from behind. (16) Thoracic nota. (17) Anal claw.

Summary.

The larvae of *Leptocerina ugandana* (Ulmer) and of the two subspecies, *ramosa pinheyi* Kimmins and *L. ramosa trifida* Kimmins are described and figured. The two subspecies of *ramosa* are an example of subpsecies which can only with difficulty be separated in the adult stage, but in the larval stage can be separated with ease—both morphologically and from their case-making habits.

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NOTES ON *ANOPHELES MARTERI* SENEVET AND PRUNNELLE, 1927.

By E. R. Shahgudian.[1]

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Introduction.

In the Spring of 1953 in Teheran during examination of anopheline larvae collected by one of the malaria survey teams of the Institute of Malariology from Yazd region (central plateau of Iran), I found two dozen larvae which, according to the present available keys for the Palearctic region and also some monographs, were identified as *A. sogdianus* Keshish'yan, 1938. All of them had stigmal processes as well as middle and outer prothoracic dorsal hairs arising from separate tubercles.

This year (1954) a large number of larvae and adult anopheles were collected from the same place (by Dr. Janbakhsh and others) and brought to the Institute.

In the process of identification of the second collection I was faced with a confusing problem. Nearly all larvae (about 95 per cent.) showed the characters of *A. sogdianus*, as in the previous year, while among the adults 90 per cent. had a pale apical fringe spot which is characteristic of *A. marteri* Senevet and Prunnelle. Fourth instar larval skins of *A. marteri* were examined and had characters of *A. sogdianus* as described by Keshish'yan.

It is worth mentioning that usually on the apex of the wing a conspicuous golden spot could be seen, but some specimens had a light silver-grey spot, while in a few of them (usually males) this spot was absent. The positions of the cross-veins (which have been thought to differ in *marteri* and *sogdianus*) varied ; usually the anterior and median were in the same line, the posterior vein being situated behind them, or else the anterior cross-vein was in front of the median and the posterior vein well behind it. In a few specimens the anterior cross-vein was slightly behind the median one while the posterior cross-vein was still further behind it. Some distinct *A. marteri* had cross veins which agreed with *A. sogdianus* and vice versa.

What is the solution to this problem? This is a question which is posed by many systematists working in the Palearctic region and it led me to analyse more closely the whole question of identification of these anophelines.

Geographical Distribution (Fig. 1).

Anopheles marteri has a " spotty " distribution in the mountainous areas of the countries surrounding the Mediterranean Sea ; its breeding places are similar wherever it occurs ; larvae are found in shaded mountain torrents or streams among rocks and boulders. The species appears to be of little or no medical importance.

A. marteri was first described by Senevet and Prunnelle (1927), who found it breeding in the Tell mountain region of Algeria in April, 1927. During the next twenty-seven years it was found and recorded in the following countries : Greece in 1932 (Shannon, 1933) and in 1936 (Hadjinicolaou, 1938) ; Corsica, two larvae in 1925 (Langeron and Galliard, 1933); Bulgaria in 1935 by Shannon (Hadjinicolaou, 1938); Tadjikistan, as *A. sogdianus* (Keshish'yan, 1938, 1941); Albania (Bates, 1941); Syria and Lebanon in 1941 (Leeson, 1942, Leeson *et al.*, 1950); Tunisia in 1941 (Sicart, 1942); Iran in 1942 by Macan (Leeson *et al.*, 1950), one larva in 1941 (Beklemishev and Shipitzina, 1947) and in 1953 and 1954 by Shahgudian and Janbakhsh; Transjordan and Palestine in 1941 and 1942 by Lumsden and Yofe (Leeson *et al.*, 1950); Iraq in 1942 by Macan (Leeson *et al.*, 1950); Spain in 1943 as var. *conquensis* (Torres Cañamares, 1944, 1945, 1946) and in 1946 and 1947 (Romeo Viamonte, 1950); Cyprus in 1946 (Aziz, 1947, 1948); Morocco in 1947 (Gaud, 1948); and in Sardinia, 1946–1950 (Aitken, 1954).

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[1] This work was done during my stay in the Department of Entomology, London School of Hygiene and Tropical Medicine, 1954–55, as a Fellow of the World Health Organization.

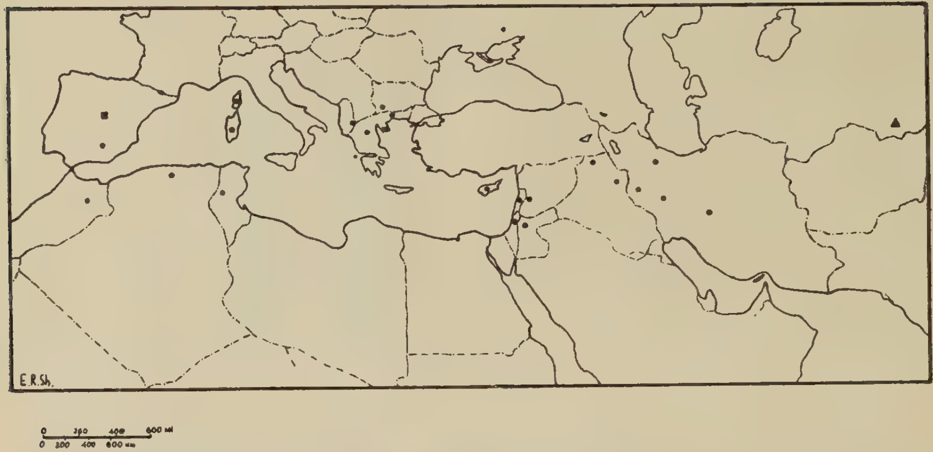

Fig. 1.—Distribution of *Anopheles marteri* Senevet & Prunnelle, 1927. ● Places from which *A. marteri* has been recorded. ■ Described as *A. marteri* var. *conquensis* by Torres Cañamares, 1946. ▲ Described as *A. sogdianus* by Keshish'yan, 1938.

Material Examined.

The *Anopheles marteri* material in the Department of Entomology, London School of Hygiene and Tropical Medicine and in the British Museum (Natural History) was not sufficient to study from all recorded places.

Larvae from Algeria, Spain (var. *conquensis*), Greece, Transjordan, Palestine, Sardinia and Iran, together with adults from Algeria, Transjordan, Iraq and Iran were closely examined and were compared with the descriptions given by the different authors.

Two important observations were soon made. Firstly, it at once became apparent that the larval material fell into two groups; those from Algeria, Tunisia (according to the drawing by Sicart, 1942), Spain, Transjordan and Palestine forming one group in which the posterior clypeal hairs were short and usually extended forward only just beyond the bases of the inner anterior clypeal hairs and not beyond the anterior border of the clypeus (fig. 2, *a*). The second group were larvae from Sardinia, Greece, Tadjikistan (according to the drawing by Keshish'yan, (1938) and Iran; the posterior clypeal hairs on these larvae were much longer, that is they extended well beyond the anterior margin of the clypeus and approximately a quarter of the way along the inner clypeals (fig. 2, *b*).

The second observation was made during the examination of morphological characters given by Keshish'yan, 1938, for differentiation of *A. marteri* and *A. sogdianus*, and by Torres Cañamares, 1946 for separating *A. marteri*, *A. marteri* var. *conquensis* and *A. sogdianus*. In the original description of *A. marteri*, Senevet and Prunnelle described (*a*) the prothoracic dorsal hair 1 as having a large tubercle, (*b*) hairs 2 and 3 arising from a common tubercle and (*c*) in the drawing (Senevet, 1935) the prothoracic dorsal hairs 5 and 6 are shown as having separate tubercles.

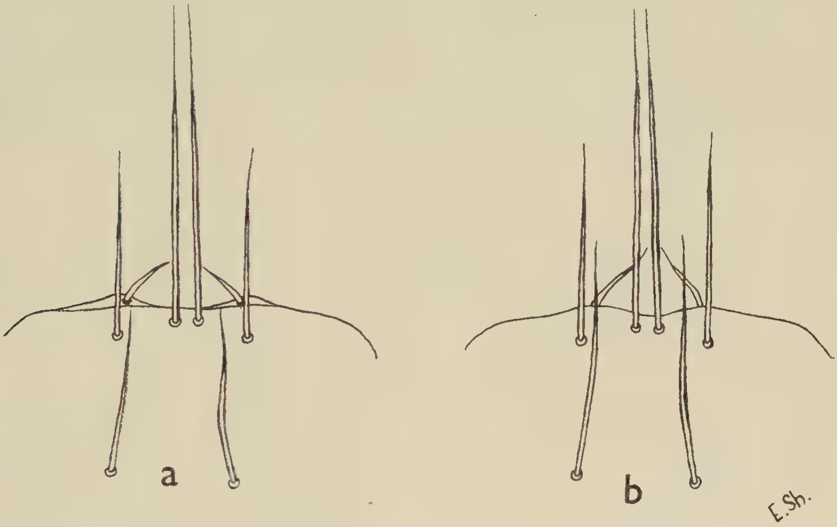

Fig. 2.—Clypeal hairs of fourth instar larva. (*a*) *A. marteri marteri*; (*b*) *A. marteri sogdianus*.

My examination of two larval skins of *A. marteri* collected in Algeria in 1927 by Senevet, which are now in the British Museum (Natural History), showed strong evidence that most of the figures had been drawn from one of them. In this one the thorax was so distorted that the dorsal hairs were displaced. An error was thus made in the description and in the drawings which undoubtedly led Torres Cañamares to name the Spanish specimen as var. *conquensis*, and I suspect that the statement of Keshish'yan about the absence of stigmal processes in the Algerian *A. marteri* was also based on Senevet's (1935) drawing in which the processes are omitted.

Adults examined had no pre-stigmal hairs; an anterior tuft was present with 7–15 flattened light chaetae. The palpi (male and female) were as long as the proboscis or slightly shorter; cross-veins were variable in position; the light fringe spot on the apex of the wing varied from golden or light yellow to silver-grey, in some specimens it was absent.

Since there is no controversy on the hypopygium and pupa of *A. marteri*, *A. marteri* var. *conquensis* and *A. sogdianus* and their external morphology seems to be identical, the writer finds it unnecessary to describe them.

CONCLUSIONS.

(1) The examination and comparison of the larvae of *Anopheles marteri* Sen. & Prun. from Algeria with larvae of *A. marteri* var. *conquensis* from Spain has revealed no differences. The original descriptions of adults of *A. marteri* var. *conquensis* Torres Cañamares apply equally well to *A. marteri* from Algeria. There appears to be no necessity therefore to distinguish these forms on morphological grounds and it is proposed that the varietal name be sunk as a synonym.

(2) Larvae of *A. marteri* from Algeria, Tunisia, Spain, Transjordan and Palestine are characterised by having shorter posterior clypeal hairs than those from Sardinia, Greece, Tadjikistan and Iran, and it is proposed that the first group should be regarded as typical of the species described by Senevet and Prunnelle and should retain the name *Anopheles marteri* subspecies *marteri.*

The forms occurring in the second group of countries are more nearly related to that described by Keshish'yan as *Anopheles sogdianus,* and it is proposed that this group should therefore be named *Anopheles marteri* subspecies *sogdianus.*

(3) No constant morphological differences could be detected in other stages of these anophelines.

ACKNOWLEDGMENTS.

I wish to express to the late Professor P. A. Buxton, C.M.G., F.R.S., Director of the Department of Entomology in the London School of Hygiene and Tropical Medicine and to Major H. S. Leeson, F.R.E.S., my deep appreciation and thanks for the help and guidance afforded me in this investigation.

I am also grateful to Professor N. Anssari, Director of the Department of Parasitology in the Medical School of Teheran University and Director of Institute of Malariology, for his encouragement and interest in my work.

To the Keeper of Entomology at the British Museum (Natural History) I am grateful for permission to examine the material in the National Collection and to Mr. P. F. Mattingly of the Department of Entomology I am indebted for valuable advice and assistance.

I wish also to acknowledge with thanks the kindness of all those who sent me material for examination, including Dr. Sh. Mofidi and Dr. N. Ghaffary of Institute of Malariology, Teheran, Iran ; Prof. G. Livadas of School of Hygiene, Athens, Greece ; Dr. T. Cañamares, Jefe de Sanidad Quenca, Spain, and Dr. C. Cantini, Centro Regionale Antimalarico, Sardinia.

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ON THE LARVA OF *CRYPTOHYPNUS QUADRIPUSTULATUS* FABRICIUS (COLEOPTERA : ELATERIDAE).

By the late A. W. Rymer Roberts, M.A., F.R.E.S.

During the late war the Ministry of Agriculture's scheme of soil-sampling, to determine the number of wireworms in newly-ploughed grassland, has led to the discovery of the larvae of several species of Elateridae, amongst them those of *Cryptohypnus quadripustulatus* Fabricius. In February, 1940, the first specimens of this species were found by Petherbridge and Stapley in the light soil of the Breckland, near Newmarket. Later in the same year the same workers took considerable numbers in Soham Fen, Cambridgeshire, and at about the same time Dicker and Smart took specimens at Hawthorn Hill Racecourse, Berkshire. From both places the finders preserved some larvae alive and reared adults, identified as this species by myself and Dr. van Emden respectively. Larvae have since been reported from three localities in Derbyshire by Roebuck and Bray (1944), Yorkshire (Cooper, 1945), Leicestershire and Devonshire (van Emden, 1945).

Cryptohypnus quadripustulatus Fabricius

Larva.

Length of larva in final instar 6–8 mm. Biconvex ; creamy-white, except head and prothorax, which are yellow. Not strongly corneous. Ninth abdominal segment with a pair of inwardly turned pseudocerci, almost completely enclosing a heart-shaped space.

Head (fig. 1) nearly equally long and broad, its sides subparallel. Cranial sutures widely separated in front and inclined together backwards in a narrow V-shape almost to the occiput. Ventrally the sides of the submentum are slightly separated. Setae mostly short, but with two long ones on either side mid-way between the anterior and posterior margins. *Ocelli* absent. *Antennae* 3-segmented ; third segment nearly cylindrical and bearing rather long setae ; accessory segment conical. *Nasale* (fig. 2*b*) bearing three sharp teeth almost equal in length and four small blunt teeth or processes behind the anterior margin ventrally. The anterior part of the epistome on either side is not produced forwards quite so far as the apices of the three teeth and bears a tuft of inward-bending hairs. The epistome bears, in addition, a transverse row of eight setae, mostly rather long. *Mandible* (fig. 4) arcuate and somewhat slender, with a single-pointed brown apex, on the inner margin of which is a slight flange or obtuse tooth. Near this flange is a short, pointed retinaculum, followed by five or six smaller serrations up to the middle of the inner margin. At the base there is a tuft of long hairs (the penicillus).

Maxilla.—Cardo partly infolded, slender, triangular, with apex reaching to gula. Stipes elongate, rounded on outer, straight on inner margin. Palp long, 4-segmented, borne on a raised palpiger. Mala (fig. 2*a*) unjointed, rather slender, bluntly pointed at the apex and bearing some six long, stiff setae and, near the apex, a small circular sensillum. No lacinia is developed. From the base of the mala to the hypopharynx the inner margin of the stipes is densely clothed with long hairs.

Labium with biarticulate palpi and small rounded ligula ; mentum short and colourless, submentum long, parallel-sided. The outer margin of the anterior segment of each palp bears a short stout spine not far from its base. *Gula* narrow, subparallel, but slightly widened anteriorly and posteriorly.

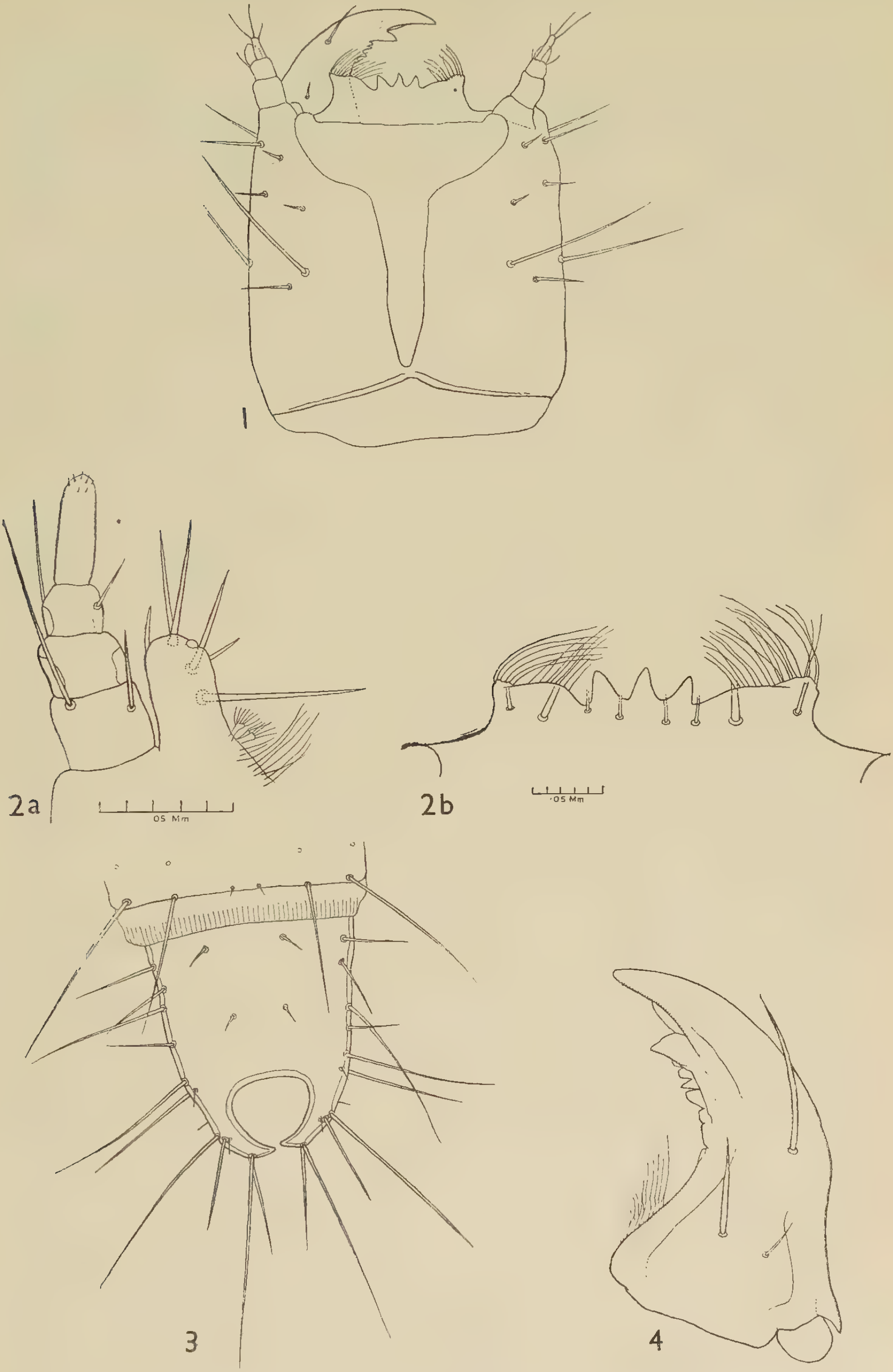

Fig. 1–4.—*Cryptohypnus quadripustulatus* Fabricius. (1) Head, dorsal aspect (right mandible omitted). (2*a*) Maxilla, ventral aspect; (2*b*) nasale, dorsal aspect (setae broken). (3) Terminal segments. (4) Right mandible, dorsal aspect.

Prothorax, the longest segment of the body, bears a marginal border of faint longitudinal striae anteriorly and posteriorly, on praenotum and postnotum respectively. Pronotum with three transverse rows of setae, the intermediate row short. *Meso-* and *metanotum* not much more than half the length of pronotum. They and *abdominal tergites* with only two transverse rows of setae. Longitudinal striae present only on anterior margin. No muscular impressions visible. *Pleura* wider posteriorly than in front, each bearing scattered setae, of which one is longer than the rest. *Legs* rather widely separated, each bearing a few setae, and on the inner side of trochanter, femur and tibia short, stiff spines. Claws rather long and slightly curved.

The tergo-pleural suture is difficult to define. Thoracic and abdominal *sternites* with three transverse rows of setae, the posterior row the longest. *Ninth abdominal tergite* more flattened than the rest, but slightly convex. Its surface almost without sculpture. The margin bears some ten long, finely tapered setae, together with two or three minor setae on either side, and there are a few other long setae ventral to the marginal rim. Two pairs of short submedian setae present, one slightly longer near the anterior margin, the other shorter, a little anterior to the posterior space. This is rounded, somewhat heart-shaped and enclosed almost completely by the two pseudocerci. The latter bear long setae (included in the number for the segment) and terminate each in a single point. The pleura form an arch surrounding the ninth sternite and tenth segment (pseudopod) ventrally, the ninth tergite extending laterally to their margins. *Spiracles* biforous and extremely small: the two chambers elongate-oval, their margins thickened at the sides and bearing up to six supporting spines on either side, almost colourless. The mesothoracic spiracles lie laterally of the anterior part of the segment on either side. Abdominal spiracles lateral in paratergite, similarly to the thoracic. The scar anterior to the chambers in each case, yellowish.

RELATED SPECIES.

I am greatly indebted to Dr. Robert Glen, then of the Dominion Entomological Laboratory, Saskatoon, for sending me a copy, with photographs, of the figures of that part of his thesis on the larval morphology and taxonomy of the tribe Lepturoidini which deals with *Cryptohypnus* and *Hypnoidus*. In it Glen divides the species which he has examined between the two genera *Cryptohypnus* and *Hypnoidus*.

In *Cryptohypnus* Esch. he includes *riparius* Fab. from Europe and four species from North America; *Hypnoidus* Steph. includes *maritimus* Curtis from Austria, *dubius* Horn and *musculus* Esch. from N. America. Some of the distinctive larval characters which he gives for *Hypnoidus* are: the form of the mandibles, each bearing a small retinaculum with fine serrations posterior to it; the absence of spine-like setae on the coxa; the pointed undivided urogomphi; the three short subequal teeth of the nasale; the fronto-clypeal area pointed posteriorly; the absence of ocelli. All these characters are also borne by *quadripustulatus* and it must, on the larval characters, evidently be included in the same group or genus.

In addition Dr. Glen informs me in his covering letter that the maxilla of each of the three species of *Hypnoidus* examined by him bears a single unjointed mala only, as in *quadripustulatus*, and not the two-jointed galea and hairy lacinia of *Cryptohypnus riparius*, usual in Elaterid larvae. This latter character was apparently used by Böving and Craighead (1931 : 11) (as well as by Schiödte) as one of those distinguishing their super-family Elateroidea and it has been accepted as such by many workers on these larvae. It is, therefore, a matter of considerable interest that a group or genus in this large super-family should have diverged so much in what is considered an important larval character.

To the same group must also be assigned *C. dermestoides* Hbst., the larva of which was found by Messrs. Roebuck, Bray and Broadbent (van Emden, 1945).[1] Through the good offices of Dr. van Emden I have been enabled to examine the larva deposited by Broadbent at the British Museum and find that, as would be expected from its position in the former's key (1945), this species also possesses a single maxillary mala, as do the other species named above.

It is of interest to note that, though the differences between these two genera are not very great in the adult stage, and though the larvae of *Cryptohypnus* in the present sense were unknown to them, Reitter (1911) and Henriksen (1913) have both separated genera, though they differ in the nomenclature used. Moreover, Stephens (1830) expected that his genus *Hypnoidus* would be divided before long and specified characters in the antennae of the adults for the separation of the British species into the two groups.

With some hesitation I have decided to follow the nomenclature used by Henriksen (1913), Hyslop (1921) and van Emden (1945), reversing with regret the names given by Glen to these two genera. Thus *Hypnoidus* Steph. is reserved for the group of which *H. riparius* Fab. is the type and *Cryptohypnus* Esch. for that including *C. quadripustulatus* Fab., *C. dermestoides* Hbst., *C. maritimus* Curt., *C. dubius* Horn and *C. musculus* Esch.

Little is known of the biology of this species, nor whether it can be considered as injurious to crops. Larvae have been taken from light soils and from fenland, though the species is said to be associated with rivers. Pupation takes place in spring and adults emerge from about the 20th May to early June.

ACKNOWLEDGMENTS.

It is a pleasure to record the valuable help I have received from my friend, Dr. F. I. van Emden. We have both investigated independently larvae from the two first sources, he those from Berkshire found by Dicker and Smart and I those of Petherbridge and Stapley from the Breckland and Fens, as well as Berkshire specimens. Yet at no time was there competition for priority but rather co-operation in every possible way.

To the finders of these first larvae I am also indebted for specimens and for their patience in waiting so long for a description of their specimens.

I must acknowledge again the courtesy of Dr. Robert Glen, of the Canadian Entomological Service, in providing me with descriptions of related forms in so generous a manner.

Finally, to Mr. Terzi I am deeply indebted for his care and masterly skill in finishing the drawings inadequately prepared by myself.

SUMMARY.

The larva of *Cryptohypnus quadripustulatus* Fabricius is described from material found in the Eastern and Home counties of England. Attention is particularly drawn to the fact that in this genus, so far as known, the maxilla

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[1] It appears probable now that this larva, described as *C. dermestoides* Hbst. in 1945, is in reality *C. sabulicola* Boh. (F. V. E., 15.ii.56).

is provided with a single mala in place of galea and lacinia, as found in *Hypnoidus* and all other known species of Elateridae.

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NOTES ON MICROCLIMATE AT THE SITES OF BREEDING AND BITING OF *AËDES* SPECIES (DIPTERA : CULICIDAE) ON UKARA ISLAND, TANGANYIKA.

By A. Smith, PhD.

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Introduction.

The results presented here are a preliminary report. These previously unpublished observations were made during a period of residence on Ukara Island which is situated in Lake Victoria at 1° 8′ S., 33° 05′ E. and is described by Smith (1955).

Climatic Conditions at the Site of Breeding.

Three breeding places of *Aëdes*, situated within a few yards of one another, were chosen for examination and water temperatures taken with a glass-sheathed thermometer capable of giving readings to a quarter of a degree centigrade. Intensities of reflected light were determined by holding the selenium cell of an autophotometer one foot above the surface of the water where this was possible at two of the sites. The observations were made during one day in the long rains in May and extended from 8 a.m.–3 a.m. The three sites were :

(1) A rock pool—containing larvae and pupae of *Aëdes vittatus* Big.

(2) A mango tree the divided trunk of which contained a pool with larvae and pupae of *Aëdes africanus* Theobald, *Aë. aegypti* L. and *Aë. apicoargenteus* Theobald.

(3) A rot hole in a pollarded tree with larvae of *Aë. africanus* and *Aë. apicoargenteus*. The climatic measurements in Table I show that the temperature of the water in which *Aëdes vittatus* breeds rose 5° C. above that of air temperature during the hottest part of the day, whereas the temperature of the water in rot holes with *Aë. africanus* and *Aë. apicoargenteus* larvae was nearly 1° C. colder than air temperature. These differences can be accounted for by the rock absorbing radiant heat during the daytime, thus raising the *A. vittatus* breeding site above air temperature. Insulation of rot holes against radiant heat by the tree would prevent heating of the breeding site and evaporation from the trunk reduce the water temperature below air temperature.

Reflected light from the rock pool was of the order of 60 F.C. compared with 2 F.C. at the surface of water in the mango tree, during the brightest parts of the day. Temperature as well as light conditions are extremely stable at the site of a rot hole compared with the rock pool. The temperature varied 4·5° C. in the rock pool compared with 1° C. in the mango tree and 2° C. in the pollard over the period of the observations.

Climatic Conditions at the Site of Biting.

Four pairs of boys sat near pollarded trees inside a circular boma enclosing three huts. One African acted as bait and the other caught mosquitoes alighting

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[1] Now Entomologist, Pare Malaria Scheme, East Africa.

PROC. R. ENT. SOC. LOND. (A) 31. PTS. 4–6. (JUNE, 1956).

TABLE I.—*Giving microclimate at* Aëdes *breeding sites from 8 a.m.–3 a.m.*

Site.		a.m.					p.m.												a.m.		
		8.	9.	10.	11.	12.	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	1.	2.	3
Rock pool . .	Temp. (°C.)	23	23.5	24	23	23.5	25.5	27	27	27	27	25	24	23.5	23.5	23	23	23	23	22.5	22.5
	Light (F.C.)	20	25	35	10	40	60	60	50	52	30	16	0	0	0	0	0	0	0	0	0
Rot hole in Mango tree	Temp. (°C.)	21	21	21	21	20.5	20.5	20.5	20.5	20.75	21	20	21	21	21	21	21	21	21	21	21
	Light (F.C.)	0.4	0.4	2.0	0.8	1.2	1.6	2.0	2.4	2.4	2.0	1.0	0	0	0	0	0	0	0	0	0
Pollard . . .	Temp. (°C.)	20	20.5	20.5	20.5	20.5	21	21	21.5	21.75	22	22	22	21.5	21.5	21	21	21	20.5	20.5	20.5
Outside . .	Temp. (°C.)	21	22	23	20	21	23	22	22	22	23	21	20	21	21	21	21	21	21	21	21
	Light (F.C.)	100	100	100	100	190	200	180	180	140	135	54	0	0	0	0	0	0	0	0	0

TABLE II.—*Showing microclimate at four sites of biting of* Aëdes *species during different times of the day.*

Climatic conditions.	11 a.m.				12 a.m.				1 p.m.				2 p.m.				6 p.m.			
	1.	2.	3.	4.	1.	2.	3.	4.	1.	2.	3.	4.	1.	2.	3.	4.	1.	2.	3.	4.
Light falling vertically	80	150	260	130	50	60	210	90	.	.	.	.	.	90	50	.	32	40	40	32
Light reflected from bushes 3 ft. away .	50	30	20	70	40	30	40	60	.	.	.	.	.	50	20	.	12	8	6	22
Illumination amongst foliage . . .	.	.	.	.	.	.	.	.	20	30	2	60	.	40	5	.	6	20	2	18
Temperature (° F.)	76	76	76	75	79	78	78	78	.	.	.	.	.	89	77	.	75	75	76	75
Relative humidity	83	83	87	83	80	72	80	80	.	.	.	.	.	49	76	.	83	83	78	83
Light reflected from subject at 3 ft. away .	20	30	50	40	20	20	40	40	.	.	.	.	.	22	20	.	8	6	12	14

on him in test tubes and with the aid of a torch at night. Collections were made during two days in April. One of the eight catchers (No. 3) consistently caught more *Aëdes* than the other catchers. His total was 225 compared with 153 caught by the other pairs together. A comparison of the climatic conditions at the four sites of collecting shows that at site 3 the intensity of illlumination was much lower among the foliage than at the other sites. Other climatic conditions were not consistently different (Table II). Light is measured with an autophotometer and temperature and humidity with a whirling psychrometer swung among the foliage.

If, as it appears, the incidence of biting activity depends so much on very local conditions, then it seems likely that the human bait draws on mosquitoes within a few feet. It was noticed at site 3 that *Aëdes africanus* and *Aëdes apicoargenteus* flew out from dense bush and bit an observer sitting close by. By lying at the side of a bush, with shirt removed, one could see unfed *Aë. africanus* and *Aë. apicoargenteus* resting in the dark middle part of the bush on the edges of leaves. In a short time *Aëdes* species flew from the bush, in two cases tracing a descending spiral path. They alighted quickly, fed and some were seen to fly back to the bush, where they rested on leaves exposed to the sun or on peripheral leaves on which the sun was not shining. One gorged *Aë. africanus* remained in an exposed position for half an hour. Another, after biting and gorging, flew to a plant about six feet away and rested on the undersurface of a leaf. In many cases individual mosquitoes which alighted to bite could not be detected in their coming and going.

These observations indicate that dense thicket near a mosquito catcher is a source of unfed *Aëdes* which are resting and ready to bite any person close by.

The following observations were made to study the biting activity of *Aëdes* species in different surroundings during one day in May, 1952. The sites for studies were examined for *Aëdes* breeding places and mosquito adults bred out of water with larvae taken from the mango tree, pollarded trees and two rock pools nearby.

The following numbers were bred out :

Mango tree:	
Aë. apicoargenteus	16
Aë. africanus	1
Aë. aegypti	1
Pollards :	
Aë. apicoargenteus	6
Aë. africanus	2
Rock pools :	
Aë. vittatus	67

Five pairs, consisting of catcher and bait, collected mosquitoes biting between 7.30 a.m. and 7 p.m. The positions of the sites are described in Table III, which gives the total *Aëdes* collected.

A comparison of climatic conditions (Table IV) gives no indication that temperature, humidity or light at the positions of the mosquito catchers influence the numbers caught at different sites. Any of these factors appear to be masked during daylight hours by the presence of suitable thicket, which is a

Table III.—*Showing the total* Aëdes *collected on human bait in different surroundings.*

Site.	Position.	Species of *Aëdes.*	Number.
1	At the base of a mango tree which had a pool in its divided trunk. A little bush at the bottom of the tree and the canopy gave constant shade	*africanus*	2
		apicoargenteus	6
2	Beneath the edge of the canopy of the mango tree	*africanus*	5
		apicoargenteus	1
3	Inside and close to the thick bush of the hut boma	*africanus*	41
		apicoargenteus	34
4	In the open	*africanus*	5
		apicoargenteus	4
5	Close to rocks, near bushes and shaded by two trees	*africanus*	39
		apicoargenteus	33
		aegypti	7
		vittatus	1

Table IV.—*Giving the climate at five sites of* Aëdes *collection.*

		a.m.					p.m.						
Site.	Climate.	8.	9.	10.	11.	12.	1.	2.	3.	4.	5.	6.	7.
1	Temp. °F.	72	72	73	69	70	70	72	72	72	73	71	69
	R.H.	83	83	83	95	86	91	83	83	83	83	87	95
	Light F.C.	50	60	55	26	90	120	110	85	80	85	30	0
2	Temp. °F.	72	72	72	68	70	71	72	73	72	73	71	69
	R.H.	83	83	83	95	91	87	83	83	83	83	87	95
	Light F.C.	100	100	70	30	130	160	155	145	120	100	44	0
3	Temp. °F.	71	72	72	68	70	72	71	72	71	73	72	70
	R.H.	87	83	83	95	91	87	87	83	87	83	83	95
	Light F.C.	40	40	50	50	110	110	80	80	65	60	18	0
4	Temp. °F.	71	72	73	68	71	73	72	72	72	73	71	69
	R.H.	87	83	83	95	87	83	83	83	83	83	89	95
	Light F.C.	100	100	100	100	190	200	180	180	140	135	54	0
5	Temp. °F.	72	72	72	67	70	72	72	72	72	72	70	69
	R.H.	83	83	83	100	91	83	83	87	83	83	82	95
	Light F.C.	60	60	70	60	140	70	100	120	80	75	30	0

Rain 10–12 a.m.

resting place for unfed and fed *Aëdes*, the unfed ones leaving the thicket to bite a man nearby.

An alternative explanation is that *Aëdes* are continually in flight but are unable to detect their hosts in windy places and people are located only in places sheltered from the wind. This explanation is contraindicated by the occurrence of resting *Aëdes* in bushes during daytime.

SUMMARY.

(1) Reflected light from a rock pool with *Aëdes vittatus* larvae was of the order of 60 F.C. compared with 2 F.C. above a pool in a rot hole with larvae of *Aë. africanus*, *Aë. aegypti* and *Aë. apicoargenteus* during the brightest parts of the day. Temperature varied 4·5° C. in the rock pool compared with 1° C. in a rot hole in a mango tree and 2° C. in a rot hole in a pollard.

(2) Larger numbers of *Aëdes* were caught on human bait near foliage with a dark interior (2 F.C.) than near foliage with brighter interiors (20 F.C.).

(3) Observations were made to study the biting activities of *Aëdes* species in different natural surroundings. It was concluded that any advantageous differences of temperature, humidity or light at the position of the mosquito catchers were masked during daylight hours by the presence nearby of suitable thicket, which is a resting place for *Aëdes*.

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Book Notice.

Gall Midges of Economic Importance. By H. F. Barnes, M.A.(Oxford), Ph.D.(London). Vol. VII. *Gall Midges of Cereal Crops.* With a foreword by Prof. H. W. Miles. 8vo. London (Crosby Lockwood & Son Ltd.), 1956. Pp. 261, 15 pls., 6 text-figs. Price 21*s.*

This is the seventh volume of the series "Gall Midges of Economic Importance" the first volume of which appeared in 1946.

The present volume, which deals with the gall midges of cereal crops, covers a wide range of species including some of the earliest described, most widely distributed and most injurious of gall midges.

The work is divided into four sections under the following headings: I: Gall midges injurious to Wheat, Barley, Oats and Rye. II: Gall midges injurious to the Sorghums. III: Gall midges injurious to the Panicum Millets. IV: Gall midges injurious to "paddy" or Rice.

The text is illustrated by 15 half-tone plates. A very comprehensive bibliography (526 titles), an index of generic, specific and popular names of Gall midges, a plant index and a general index complete the work.

THE ETHIOPIAN PENTATOMOIDEA (HEMIPTERA): XXII, ON *DISMEGISTUS* AMYOT AND SERVILLE (CYDNIDAE).

By Dennis Leston, F.R.E.S.

Introduction.

Amyot and Serville (1843) erected the genus *Dismegistus* and placed it in Cydnidae, Sehirinae (adopting present-day nomenclature); in this they were followed by Dallas (1851), Dohrn (1859) and Stål (1865, 1876). The characters uniting the genus to Sehirinae were the spiny tibiae, almost completely hidden second sternum, somewhat thickened tarsi, apically narrowed scutellum and uncompressed tibiae and femora.

Signoret (1881), at the commencement of his revision of Cydnidae, rejected *Dismegistus* on the shape of the head and the small, scarcely visible, metathoracic ostioles, placing the genus in Strachini (Pentatomidae, Pentatominae). Later authors, including Lethierry and Severin (1893), Distant (1900), Bergroth (1908), Kirkaldy (1909) and Jeannel (1913), followed this course, although Oshanin (1916) listed the genus in Cydnidae, following Stål.

Bergroth (1923) reviewed the problem and placed the genus, with *Parastrachia* Distant (an aberrant genus from Japan), in Amyoteinae (Asopinae), stressing the somewhat thickened rostrum and shape of the bucculae. Both *Dismegistus* and *Parastrachia* have a small ostiole placed close to the metacoxae and Oshanin (1922), reviewing the latter genus, placed it in Strachini, erecting a new group, Parastrachiaria, for it: he omitted to mention *Dismegistus*. Hesse (1925) retained the genus in Pentatominae.

Comparative Morphology.

It has been shown above that there are three views as to the systematic position of *Dismegistus*: (1) Cydnidae, Sehirinae; (2) Pentatomidae, Pentatominae near Strachini; (3) Pentatomidae, Amyoteinae. Rather than a generic re-description, a review of certain morphological features is presented in order to demonstrate if any of these hypotheses is correct.

Head.—The upper surface is devoid of paired bristles or marginal setae, whilst the paraclypeal lobes, although slightly longer than the clypeus, do not meet to any extent anteriorly (fig. 1*a*). The maxillary plate is without tubercles and the bucculae are low and opened behind (fig. 1*b*). The rostrum is not greatly thickened and is straight, reaching in the different species to about the mid-coxae. Mandibular and maxillary levers have been examined but lack of knowledge as to their variation within Pentatomoidea excludes them from the present analysis. The antennae exhibit a scape, bi-annulate pedicel and bi-annulate flagellum; they are slender (fig. 1*c*). Ocelli are present.

The absence of cephalic bristles or setae excludes *Dismegistus* from Cydninae; the absence of maxillary plate tubercles from Acanthosomatidae; the posteriorly open bucculae from Amyoteinae. Such subfamilies of Pentatomidae *sensu lat.* as Tessaratominae and Dinidorinae are excluded from consideration by the length of both bucculae and rostrum, whilst the comparative shortness of the paraclypeal lobes excludes Pentatominae, Phyllocephalini. Thus the head is consistent with both Sehirinae and Pentatominae. That its surface is almost

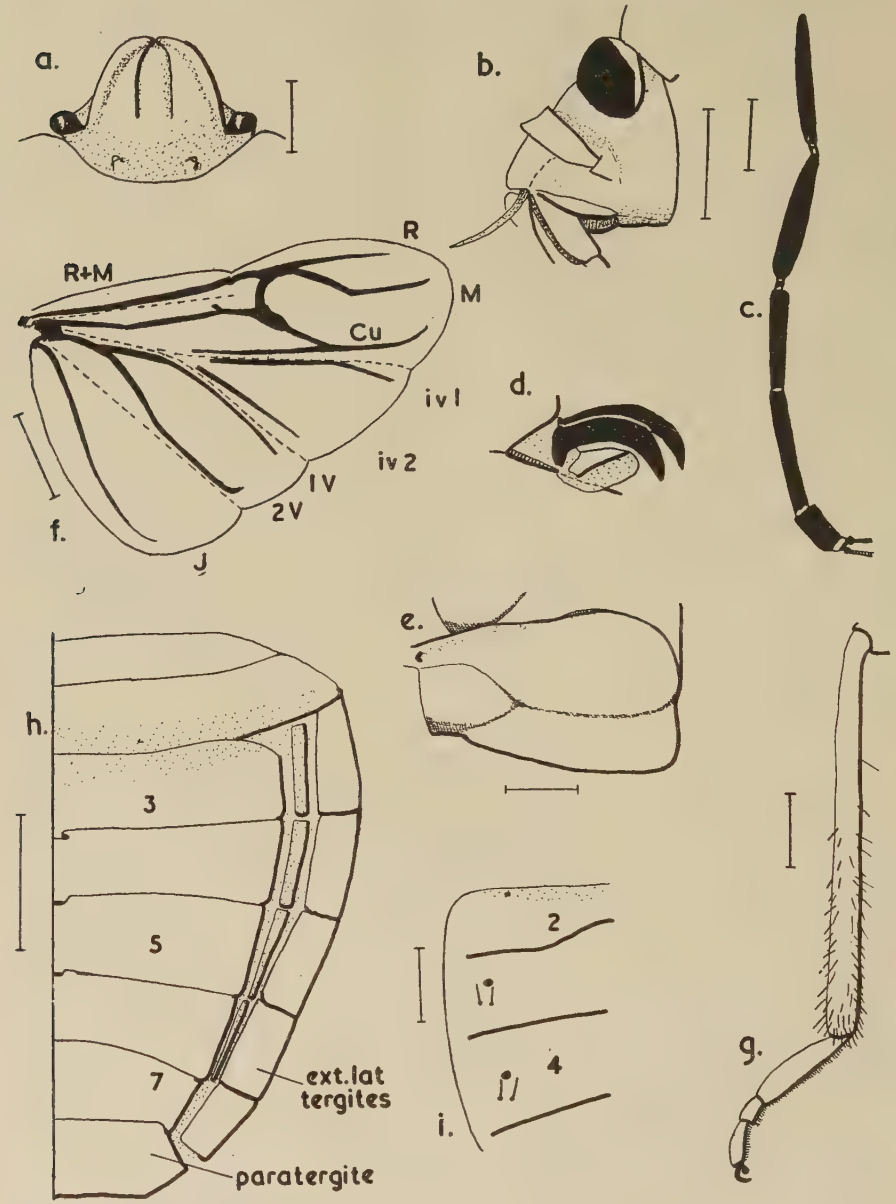

Fig. 1.—*Dismegistus binotatus* (Westwood) : *a*, head, dorsal ; *b*, head, oblique lateral ; *c*, antenna ; *d*, pretarsus and claws ; *e*, metathoracic gland opening and evaporatorium ; *f*, hind wing ; *g*, hind tibia and tarsus ; *h*, abdomen, dorsal ; *i*, abdomen, parts of terga 2–4, ventral. Scales : *a*, *b*, *c*, *e*, *g*, *i* = 1 mm. ; *f*, *h*, = 2 mm.

impunctate and a glossy shining black are points in common with many Strachini but clearly of no taxonomic significance.

Thorax and legs.—The pronotum is without paired setae. The external metathorax is scarcely modified to form an evaporatorium, whilst the gland ostiole is very small and situated between the coxal cavities (fig. 1*e*). The coxae carry a row of bristles at the distal end ; the femora are neither incrassate nor explanate, whilst the tibiae bear a number of small rigid spines (fig. 1*g*). The three-segmented tarsi are moderately thickened and the pretarsi of usual Pentatomoid form (fig. 1*d*).

The presence of spiny tibiae is indicative of a relationship with Cydnidae for, outside Cydnidae, spiny tibiae are confined to certain genera of Pentatominae, Sciocorini. McAtee and Malloch (1933) show that the presence of a row of coxal bristles is diagnostic of Cydninae, Sehirinae, Corimelaeninae and certain odd genera of unknown, but probably Cydnoid, affinities, viz. *Carrabas* Distant and *Strombosoma* Amyot and Serville. That the tibiae are not thickened apically and the tarsi non-linear excludes *Dismegistus* from Cydninae, as does the absence of paired notal setae, whilst the three-segmented tarsi differ from the two-segmented tarsi of Brachyplatidae.

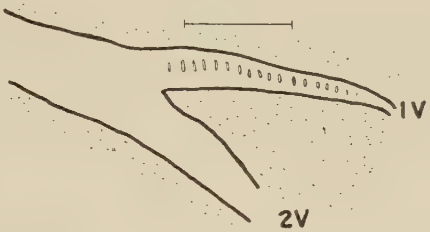

Fig. 2.—*Dismegistus fimbriatus* (Thunberg) : wing-strigil. Scale = 0·2 mm.

Wings.—The fore wings present few positive features. The anterior furrow is, apically, some distance from the costal margin, whilst the veins present (seen from the lower surface) are merely R + M and Cu. There is no definite pattern in the traces remaining of trans-membranal venation. The hind-wing (fig. 1*f*) is typically Pentatomoid but R + M and Cu are parallel for most of their course whilst a hamus is present. There is a wing strigil in all species, except *D. sanguineus*, on the proximal part of IV at and beyond the bifurcation (fig. 2).

The parallel courses of R + M and Cu excludes close relationship with Tessaratominae but the distance apart of the two veins probably also excludes Pentatominae (cf. Leston, 1953*a*, 1954*a*). Wing strigils on IV occur in Corimelaeninae, Cydninae, Sehirinae and some Tessaratominae (Leston, 1954*b*) but in the last named are correlated with the presence of a lima on the first tergum which is absent in *Dismegistus*. The somewhat featureless fore wing is consistent with most Cydninae and Sehirinae : in Amyoteinae there are usually some five or six readily visible transmembranal veins. Strong transmembranal venation of two types, with or without basal cells, characterises the two branches of Tessaratominae and strongly differentiate this subfamily from the genus under discussion (Leston, 1955).

Scutellum.—In *Dismegistus* the scutellum is longer than the basal width, moderately rounded at the anterior margins and somewhat narrowed apically. It is thus consistent with Sehirinae rather than Cydninae but, admittedly, it is not a character of great weight, However, the scutellum is quite unlike that of Scutellerinae, Podopinae, Tessaratominae, Dinidorinae and many other groups but could fall within Sehirinae or Pentatominae.

Abdomen.—Seven terga make up abdominal segments 1 to 7 ; tergum 8 is deflected downwards and in females carries ventrally the (presumably) fused paratergites of the venter (fig. 1*h*). The dorsum is highly flexible due to the great development of the lateral intersegmental membranes and desclerotisation of the posterior part of tergum 2 and the anterior part of tergum 3. The external lateral tergites (connexivum) are broad, whilst largely desclerotised internal lateral tergites are present on segments 3 to 6. The dorsal abdominal glands are persistent (at least the sacs are even though they may be non-functional) and single, being placed at the mid-line with little lateral spread. The orifice of the anterior gland is paired (secondarily) but the middle and posterior openings are single, transverse and median. The desclerotisation submarginally of segment 3 may perhaps be correlated with folding of tergum 2 over tergum 3 to form sublateral resonance chambers : this feature is less marked in the mute *D. sanguineus*.

The sterna are fused laterally and the whole venter is comparatively rigid. The spiracle to sternum 2 lies anteriorly in a membranous strip, whilst the trichobothria of sterna 2 to 7 are paired and situated side-by-side (fig. 1*i*).

Studies of the Heteropterous abdomen are almost non-existent ; however, the resonance chamber and its concomitant dorsal modifications are identical with those found in *Sehirus* (Leston, 1954*b*). Dupuis (1947, 1949) has proposed a tentative grouping of Pentatomoidea on the forms taken by the internal lateral tergites ; this work has since been extended (Leston, 1952, 1954*c*) but, whilst the internal lateral tergites are consistent with those of Sehirinae, especially in their width, they differ scarcely at all from those of Pentatominae, Acanthosomatidae and even Dinidorinae. The absence or presence of internal lateral tergite 2 is not considered of any phylogenetic importance and it is noteworthy that in *Piezosternum* Amyot and Serville, a primitive Pentatomoid in many ways (Leston, 1955), the internal lateral tergites reach the ultimate in their development, being fused longitudinally into a narrow rod.

The dorsal glands of Sehirinae and Cydninae have not, it seems, been studied previously. Examination of *Sehirus bicolor* (L.) shows these glands opening on the mid-line by narrow vents, as in *Dismegistus* ; in Pentatominae the vents are considerably wider, whilst in some subfamilies the paired openings of the anterior gland, here split into two, are as near to the connexivum as to the mid-line (Dupuis, 1947). Thus the abdomen of *Dismegistus* is consistent with its being allied to Sehirinae rather than to any Pentatominae or Amyoteinae. McAtee and Malloch (1933) show that in Cydninae and Corimelaeninae the paired trichobothria are situated longitudinally and in Sehirinae transversely, as in *Dismegistus*.

Male genitalia.—The eighth segment is reduced, without a sclerotised tergum and with small spiracles (fig. 3*g*). The ninth segment is without parandria and carries a pair of apically biramous harpagones (fig. 3*b*, *f*). The aedeagus is remarkable : the vesica and median conjunctival appendage (median penis lobe) form an elongate tube with the reservoir lying within it and opening directly to the exterior via a wide gonopore (fig. 3*a*, *e*). When retracted the vesica lies within a sheath formed probably by a pair of fused appendages. Two pairs of true conjunctival appendages are present; a dorsal pair of sclerotised rods and a ventro-lateral pair of semi-membranous appendages. The basal plate has not been studied in detail for basic studies are still needed of its homologies: a short pair of dorsal connectives (capitate processes) is present, whilst the ventral connectives are strong rods fixed tightly to the inner wall of the genital atrium.

Pruthi (1925) showed two pairs of conjunctival appendages present in *Sehirus* whereas Leston (1954*d*) has demonstrated the presence of three. He noted, however, " long chitinous struts " to the basal plate and also the small reservoir. McAtee and Malloch (1933) dealt with Corimelaeninae—a group clearly lying within Cydnidae on the presence of a wing-strigil and spiracles on a membranous strip of sternum 2 anteriorly—and figured " lateral subbasal processes " that are the ventral connectives of the basal plate. In *Sehirus* (Leston, 1954*d*) there are (1) a pair of lateral conjunctival appendages identical in general form and position with those of *Dismegistus*; (2) a pair of rod-like appendages, curved, as in *Dismegistus*; (3) short (but sclerotised) dorsal connectives as in *Dismegistus* but also most other Pentatomoidea; (4) rigid, rod-like, ventral connectives as in *Dismegistus*, Corimelaeninae and Cydninae but almost invariably ligamentous in other Pentatomoidea (cf. Leston, 1953*b*); (5) a vesica elongate in form and closely invested by the median conjunctival sheath, clearly similar in general structure to that of *Dismegistus*; (6) a pair

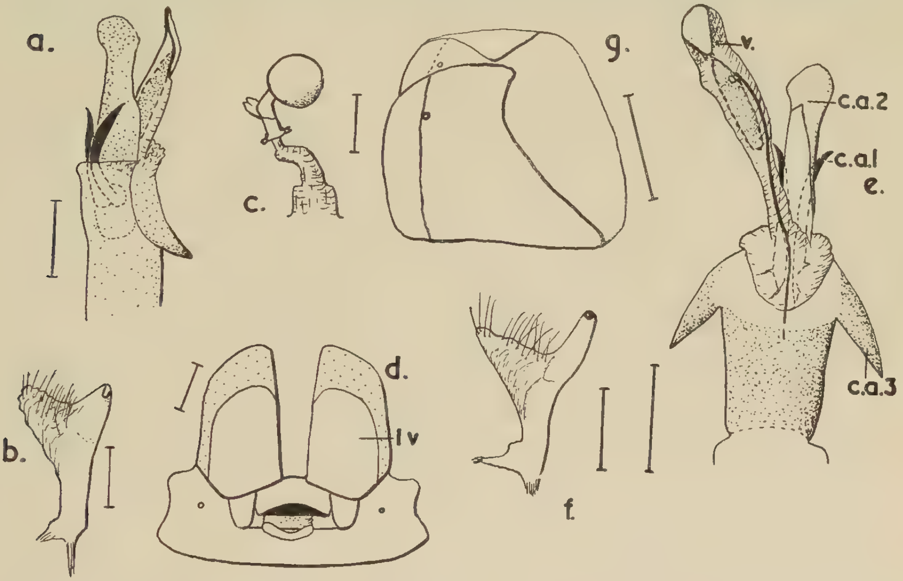

FIG. 3.—*Dismegistus binotatus* (Westwood), *a–d*; *D. fimbriatus* (Thunberg), *e–g*; *a*, aedeagus, semi-lateral; *b*, harpagone; *c*, spermatheca; *d*, ovipositor, ventral; *e*, aedeagus, ventral; *f*, harpagone; *g*, 8th male segment, oblique lateral. Scales *a*, *d*, *e*, *g* = 0·4 mm.; *b*, *f* = 0·2 mm.; *c* = 0·1 mm.

of membranous appendages originating closely to the vesica. Thus it is believed that the aedeagus of *Dismegistus* is intimately allied to that of Sehirinae: the sheath-like appendage is evidently homologous with (6) above and has originated by gradual approximation of the paired appendages at their base and eventual coalescence. It must be realised that three pairs of conjunctival appendages are the primitive armament of the Pentatomoid aedeagus (Leston, 1952, 1953*a*, 1954*a*) and, as the whole conjunctiva is merely an inflatable sac prolonging the theca (exosoma), variation within wide limits of the form taken by conjunctival appendages may occur. Indeed, reduction of this number and desclerotisation is characteristic of the Pentatominae, Amyoteinae and other higher shieldbugs, concomitantly with the evolution of sclerotised wings within the median conjunctival sheath (Leston, *unpublished*).

Biramous harpagones have evolved independently many times in Pentatomoidea—e.g., *Podops* (Leston, 1953*b*)—and, except at specific and generic level, harpagones are of little phylogenetic significance: nevertheless, it is worth noting that the harpagones of *Sehirus* are biramous. The male genitalia of *Dismegistus* are so close to those of *Sehirus*, whilst the genitalia of *Sehirus* are themselves so characteristic, that only a monophyletic origin suits the observed facts.

Female genitalia.—The valvulae have been examined and it was noted that the first rami were distinct and sclerotised; other internal structures were noted but are omitted from present consideration. The first and second valvifers are of usual Pentatomoid form but a distinct sternum and tergum (or at least a dorsal and a ventral sclerite) of segment 9 are present and the remnant of segment 10, above the anus, distinguishable (fig. 3*d*). The paratergites of segment 8 are fused to form a transverse ventral strip caudally.

The spermatheca presents a bulb, bent neck and a duct separable into three sections by virtue of different bores (fig. 3*c*). No accessory structures were noted —in KOH treated material—and the duct leads out from a large sac-like diverticulum of the vagina.

No comparative studies exist of the female genitalia of Pentatomoidea: examination of *Sehirus* shows it to be close to the pattern described both in ovipositor and spermatheca but whether this pattern may not be common to all Cydnidae awaits investigation. The spermatheca is clearly not of the form found in Pentatominae, Podopinae, Amyoteinae and Phyllocephalinae, groups possessing a highly evolved spermatheca with an elongate sac surrounding the rigid duct (Pendergrast, 1953; Leston, 1953*b*, 1954*c*): the spermatheca presents incontrovertible evidence excluding *Dismegistus* from Pentatomidae.

Systematic Position.

Dismegistus possesses no features to suggest that its affinities are other than with Sehirinae and it is therefore placed in this subfamily of Cydnidae. Once again it has been demonstrated how accurate was the work of Amyot and Serville and Stål.

Material.

The present study is based upon series of *Dismegistus fimbriatus* (Thunberg), the generotype, from Transvaal; of *D. binotatus* (Westwood) (= *sanguineus* Degeer et auctt.) from various parts of South Africa; and of *D. pauliani* nom.

nud. (from Madagascar, to be described when adequate material for a generic revision is available).

ACKNOWLEDGMENTS.

Material has been supplied by Prof. G. C. Varley, Dr. Per Brinck, Dr. R. Malaise, Dr. R. Paulian, Dr. Wallace Peters and Mr. A. L. Capener.

SUMMARY.

Dismegistus has been placed in Pentatomidae, Pentatominae ; Pentatomidae, Amyoteinae ; and Cydnidae, Sehirinae by authors. Investigation of the head, thorax, legs, wings, wing-strigil, scutellum, abdomen, dorsal abdominal glands, male genitalia, female genitalia and spermatheca confirms its position in Cydnidae, Sehirinae.

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THE RESPONSE OF A GRASSHOPPER, *ROMALEA MICROPTERA* (BEAUVOIS), TO STRONG ODOURS FOLLOWING AMPUTATION OF THE METATHORACIC LEG AT DIFFERENT LEVELS.

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In 1954 it was reported by the writer that a localised response can be obtained from *Romalea microptera* (Beauvois), a large grasshopper found in the south-eastern part of the United States, when a strongly odorous substance, such as an essential oil, is held near one of its feet. The foot tested is raised slowly and then, when the odorous substance is removed, returned to its original position. With most of the odorous materials used the response is limited to the leg tested and, providing the individual is well-fed and not subjected to additional disturbance, no other appendage is moved.

Since strongly odorous substances are stated by Dethier (1953) to be detected in insects by the receptors for the common chemical sense and, since these receptors have not, as yet, been identified with certainty for any insect, it seemed worthwhile to proceed further with these experiments in an attempt to discover the particular sense organs involved. As the first step in this direction the metathoracic legs of a number of individuals were amputated at different levels and the parts which remained were then tested as had been the intact legs in the earlier experiments. The results of this study are reported below.

Materials and Methods.

The *Romalea microptera* adults which were used in the experiments to be described here consisted of five females and five males. These were the first generation offspring of the individuals used in the previous study (Slifer, 1954). Parts of one or both metathoracic legs were cut off while the insects were in one of the later nymphal stages so that each individual underwent one or more moults after the operation. This ensured a clean stump covered with smooth cuticle. Two of the females and two of the males had parts of both metathoracic legs removed while the rest each had one normal and one operated leg. This gave a total of fourteen operated legs. Five of the fourteen legs lacked the tarsus and a portion of the lower end of the tibia, six had been amputated not far from the middle of the tibia, two retained a small portion of the proximal end of the tibia and one had been cut across near the middle of the femur. No individual was used in an experiment until it had been an adult for at least three days and all experiments were completed within twenty days after the final moult. Males and females were kept in separate cages in order to reduce stimulation by the opposite sex, and each cage was provided with large quantities of fresh food which, likewise, helped to minimise restless behaviour.

For each series of tests an individual was removed from its cage and placed on a strip of plastic screen (10 × 40 cm.) which was suspended between two ring-stands. A 60-watt electric light bulb was hung about 10 cm. above the middle of the screen while the rest of the room was in partial darkness. Under these conditions the grasshopper will usually remain quietly in the spot where it has been placed. If within a few minutes an individual did not settle down or if during an experiment it showed signs of restlessness it was put back into its cage and another animal substituted for it. Since *Romalea* is an exceptionally docile grasshopper and submits well to handling such occurrences were relatively infrequent. All movements by the experimenter when near the animal were made very slowly for such movements usually produce no response in a grasshopper.

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[1] This paper was completed in the Department of Zoology at the University of Birmingham, Birmingham, England, while the author held a Senior Fulbright Fellowship.

Clove oil, which was one of the essential oils used in the 1954 studies, was chosen as the stimulating agent. A drop of this oil was placed on a small square of filter paper which was then picked up with forceps and held close to the distal end of the leg to be tested. If no reaction occurred within twenty seconds the paper was withdrawn and the test recorded as negative. More frequently, however, a positive reaction was secured and the leg was slowly lifted into the air and then, with the removal of the clove oil, slowly returned to its original position. Each test with clove oil was preceded by a control test. This was made with a plain piece of filter paper which was picked up with a pair of forceps used for this purpose only. At the end of twenty seconds the test was recorded as either positive or negative. A period of at least five minutes was allowed to elapse between any two tests on the same appendage and only a few consecutive trials were made on any one insect in order to avoid fatiguing it. Fifty experimental and fifty control tests in all were made on each of the ten individuals.

Results and Discussion.

The results obtained with the ten *Romalea* adults tested are shown in Table I together with a summary of the results obtained for normal individuals of this species in 1954. They demonstrate clearly that sense organs capable of detecting strong repellant odours are still present on the leg even when no more than the proximal half of the femur remains.

If, now, the tests recorded earlier for intact legs (Slifer, 1954) are compared with the results in the present series it will be seen that the control tests for all appear to vary within rather narrow limits. However, if the controls for the normal and those for the amputated legs are subjected to a χ^2 test they are found to differ significantly, i.e. the individuals with the operated legs react more readily to the test with plain paper than do the normal animals. This is almost certainly not the result of the amputation itself but due, rather, to the slightly different procedures used in the 1954 and in the present series of experiments. In the earlier experiments the individuals were tested while they were resting undisturbed on the inner wall of the screened cage in which they were kept, while in the present study each grasshopper was removed from its cage shortly before being tested. There can be little doubt that the greater reactivity of the latter was due to the handling to which they had just been subjected. The difference in procedure was made necessary by the fact that a grasshopper which has a part of its leg missing usually does not keep the end of the stump close to the screen on which it is resting and so it is impossible to bring the square of test paper close to the stump while the animal is inside the cage.

In Table I it may be seen that thirteen of the fourteen amputated legs tested with clove oil as the stimulant show a smaller proportion of positive responses than did the intact legs which were studied in 1954 with this same agent. In a total of 500 tests 74·3 per cent. of the reactions were positive while in 100 tests made earlier, using this oil, 97·0 per cent. positive responses were obtained. This indicates that the leg from which a portion of its distal end has been removed is distinctly less sensitive to strong odours than is the intact leg. A χ^2 test applied to the results for the two series shows the difference between them to be highly significant with P lying well below 0·01. Again, a comparison of the present series with the total results for the 1954 studies, in which nine other odorous materials besides clove oil were used, and in which 917 out of

TABLE I.—*Reactions of* Romalea microptera *adults with metathoracic legs amputated at different levels. Drop of clove oil on filter paper square held near distal end of stump for* 20 *seconds. Stump of leg raised within* 20 *seconds in positive reaction ; no movement in negative reaction. Each experimental test preceded by a control test with plain filter paper square and positive or negative reaction within* 20 *seconds noted. R, right ; L, left.*

Condition of leg.	Control. No reaction.	Control. Postive reaction.	Experimental. No reaction.	Experimental. Positive reaction.	% of experimental tests which were positive.
Females					
No. 1 R. tarsus + tip tibia off .	24	1	8	17	68·0
No. 4 R. tarsus + $\frac{1}{5}$ tibia off .	49	1	18	32	64·0
No. 2 L. tarsus + $\frac{1}{2}$ tibia off .	49	1	23	27	54·0
No. 3 L. tarsus + $\frac{1}{2}$ tibia off .	47	3	14	36	72·0
No. 1 L. tarsus + $\frac{2}{3}$ tibia off .	25	0	6	19	76·0
No. 5 R. tarsus + $\frac{4}{5}$ tibia off .	23	2	11	14	56·0
No. 5 L. tarsus + tibia + $\frac{1}{2}$ femur off	23	2	13	12	48·0
Totals for females .	240	10	93	157	62·8
Males					
No. 1 R. tarsus + tip tibia off .	25	0	5	20	80·0
No. 5 L. tarsus + $\frac{1}{3}$ tibia off .	24	1	6	19	76·0
No. 5 R. tarsus + $\frac{1}{3}$ tibia off .	25	0	2	23	92·0
No. 1 L. tarsus + $\frac{1}{2}$ tibia off .	25	0	0	25	100·0
No. 3 R. tarsus + $\frac{2}{3}$ tibia off .	46	4	12	38	76·0
No. 4 R. tarsus + $\frac{3}{4}$ tibia off .	49	1	8	42	84·0
No. 2 R. tarsus + $\frac{4}{5}$ tibia off .	47	3	2	48	96·0
Totals for males . .	241	9	35	215	8·58
Totals for both sexes . . (operated)	481	19	128	372	74·3
Totals for both sexes . . (normal)[1]	994	6	83	917	91·7

[1] Data from Slifer (1954).

1000 tests were positive, indicates a highly significant difference to exist between these, with P extremely small. If we also take into account the fact that the control tests showed these operated animals to be more responsive to extraneous stimuli than are normal ones, as was discussed in the preceding paragraph, the difference between the operated and the normal individuals becomes even greater.

The results in Table I for the amputated legs are arranged in a graded series according to the extent of the part lost by amputation. Although the greatest decrease in sensitivity was obtained with a female (No. 5) which had the smallest portion of leg remaining there seems to be, in general, no correlation between the length of the leg left and its responsiveness. The entire tarsus, it should be noted, was missing from each of the operated legs and its absence may be the most important factor in the lowered sensitivity which follows amputation at all of the levels which were tested.

If it be assumed that a single type of chemoreceptor is responsible for the sensitivity of different parts of the leg to strong odours it is possible that the drop in sensitivity which follows loss of the tarsus, and more proximal regions as well, may be correlated with the number of these sense organs which are present on a given part and the distance between them. If, for example, the same number of receptors is present on the tibia as on the tarsus the latter might respond more readily because the sense organs on it, due to the smaller surface area of the tarsus, would, of necessity, be closer to each other. One possible explanation for the actual results obtained, then, would be that the receptors are either more numerous or else more closely placed on the tarsus than they are on the more proximal regions of the leg. An alternative explanation would be that the chemoreceptors on the tarsus are of a different type from those which occur elsewhere on the leg. Obviously, the next piece of information needed in the study of the detection of odours by grasshoppers is knowledge of the different kinds of sense organs present on the leg as well as their number and distribution. Such a study has been partially completed and it is hoped that the results will be ready for publication before long.

SUMMARY.

1. Sense organs which respond to strong odours are present on the femur, tibia and tarsus of the metathoracic leg of the lubber grasshopper, *Romalea microptera* (Beauvois).

2. After the amputation of the metathoracic leg at various levels the sensitivity of the part remaining is significantly less than is that of the normal leg.

3. It seems probable that this decrease in sensitivity is associated with either (*a*) a sparser distribution of chemoreceptors on the proximal regions of the leg in contrast to those which are more distal, or that (*b*) the sense organs on the leg which are responsive to strong odours are not all of the same type.

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AN INTERPRETATION OF THE VENTRAL REGION OF THE HYMENOPTEROUS THORAX.

By O. W. Richards, M.A., D.Sc., F.R.E.S.

It has always been difficult to homologize the parts of the Hymenopterous thorax with those of a generalized insect and some of the identifications proposed by the early workers are clearly incorrect. All the grosser errors in the thoracic nomenclature used by taxonomists were corrected by Snodgrass (1910) and some further points are explained in his book (1935). Weber (1933 : 116–197), in a work covering the whole class Insecta, incidentally deals with a number of Hymenoptera. His interpretation differs from that of Snodgrass in several important points concerning the ventral region. Since 1939, a series of papers by Ferris and his co-workers has dealt with the structure of a number of insect types (no Hymenoptera) ; for present purposes it is sufficient to quote only Ferris (1940). Michener (1944) has accepted Ferris's ideas and applied them to bees. Ferris differs most conspicuously from Snodgrass in maintaining that in most of the higher insects the sternal plates of the thoracic region have been greatly reduced or have even disappeared. Michener suggests, in particular, that the large region usually known in Hymenoptera as the mesosternum is really of pleural origin and the characteristic central longitudinal line or discrimen shows where the two pleura meet. Weber also believes that the mesosternum is reduced but he believes that the discrimen represents the line along which it has been invaginated (process of " cryptosternie ") ; according to him the sternum is still present but narrow and hardly visible externally.

In endeavouring to work out a system of homologies for the whole order none of these views has been found completely satisfactory. The proposals put forward are, however, not very different from those of Snodgrass. Two special difficulties have been noted in the course of the work. First, that an insect which has one structure in a generalised condition is usually specialised elsewhere ; it is necessary to examine a range of species to form an idea of the really generalised type which is no longer existent. Second, that differences in the thickness of the cuticle which perhaps represent relatively minor adaptations to different modes of life may greatly obscure the plan of the skeleton, especially by obliterating sutures. New suture-like structures may also arise.

(1) *The cervix and the propleuron.*

Authors do not agree as to whether the propleuron which has an unusually ventral position, only very loosely attached to its notum, does or does not include a large element derived from the cervical sclerites. Many sawflies, as shown by Ross (1937 : figs. 154–9), have a perfectly distinct pair of small cervical sclerites (fig. 3). There seems no reason to doubt that the greater part of the structures which Ross regards as enlarged cervical sclerites are, in fact, the propleuron. The division of the pleuron into episternum and epimeron is

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distinct in some sawflies (*Arge*, *Dolerus*, Snodgrass, 1910 : figs. 12 and 13) but is more often lost. In higher Hymenoptera the cervical sclerites are indistinguishably fused with the anterior end of the propleuron but it is still convenient to retain the latter name for the joint structure.

(2) *The trochantin of the first thoracic segment.*

Apparently Weber (1933 : fig. 112) is the only author who has identified rudimentary trochantins in the prothorax. Snodgrass (1910 : figs. 2, *d*) has, however, figured the same structure in *Tremex colomba* (L.). In *Urocerus gigas* (L.) (fig. 3) the trochantins are well-developed though of rather abnormal shape. The importance of this structure is that the appearance of the pro- and mesosternal regions is rather similar in *Urocerus* and what is true of one segment may be true of the next. In more specialised sawflies and in all higher Hymenoptera, the trochantin is either reduced to a minute vestige or more often has quite disappeared.

(3) *The prosternum, spinasternum and the pronotal ring.*

A plate which in sawflies lies between and behind the two propleura, but in higher Hymenoptera usually lies entirely beneath them, is the prosternum. The prosternum may appear to be partly longitudinally divided owing to a central invagination analogous to that of the mesosternum. Internally, it is produced into a strong furca whose arms arise from a common stalk. Presumably, the two apophyseal pits have been brought together and fused by the invagination of the central part of the sternum. There seems to be no compelling reason (unless by a definition devised in that sense) to hold that none of the sternum can extend laterally beyond the pits. The fore coxa in some sawflies has two articulations (Arora, 1952), one with the propleuron, the other with the prosternum. The second articulation is lost in some sawflies and probably all Apocrita.

Ross (1937 : figs. 129, 134, 136) shows that some sawflies have an intersegmental element, a spinasternum, which in some members of such families as the Xyelidae or Pamphiliidae is produced inwardly into a plate, corresponding to the more primitive spina. In more specialised sawflies, the spinasternum is fused with the front margin of the mesothorax where it is often indicated by a small central pit (Weber, 1937, fig. 153). It is highly probable that the pit (anterior discriminal pit of Michener, 1944 : 176) seen in most higher Hymenoptera in the same position is also an indication of a vestigial spinasternum.

In some members of specialised families (e.g., Cimbicidae, Proctotrupidae, Gasteruptiidae, some Apidae), the ventral corners of the pronotum are produced

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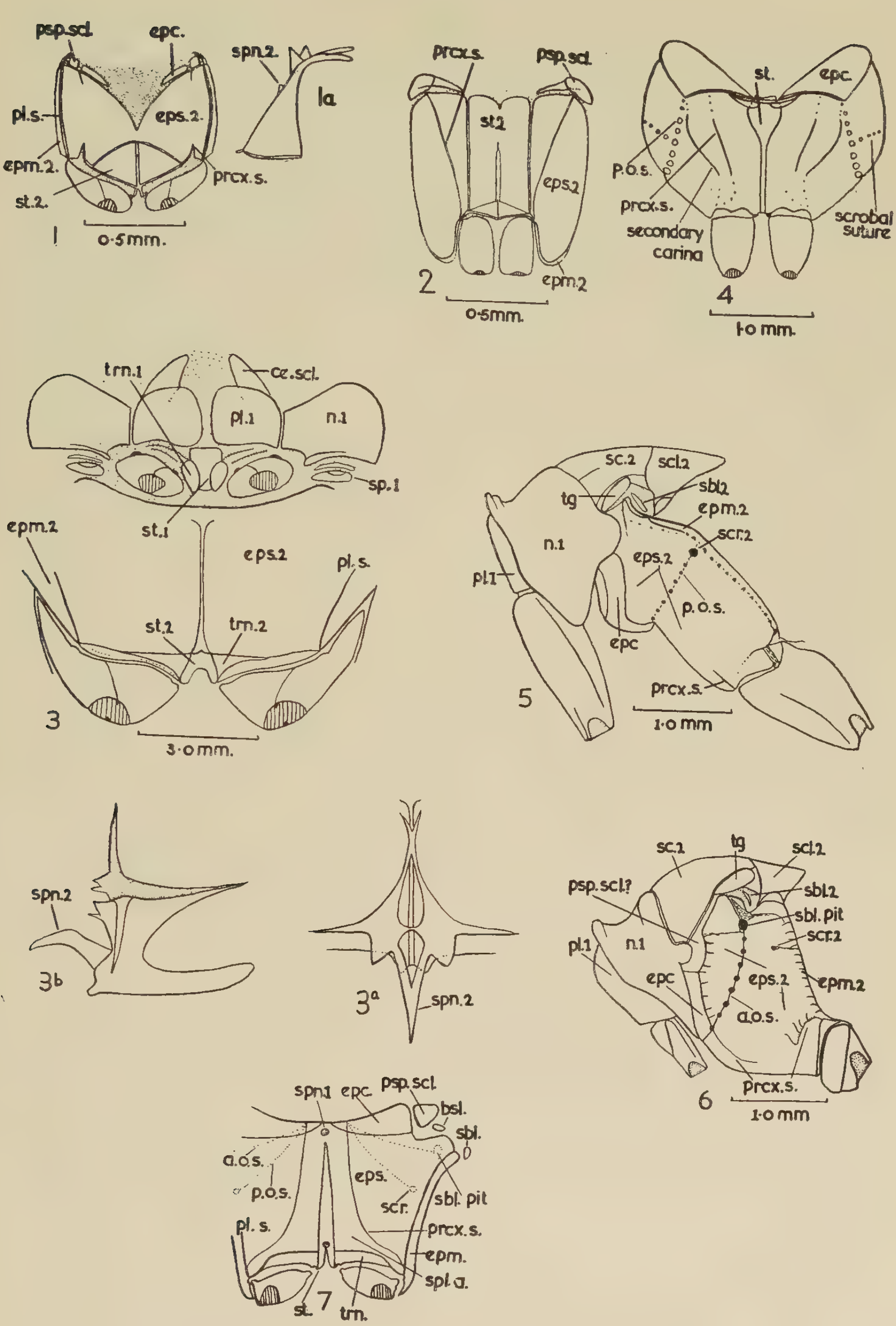
Figs. 1–7.—(1) Mesosternal region of *Xyela julii* (Bréb.) ♂ (Xyelidae). 1*a*. Mesofurca, from the right side. (2) Mesosternal region of *Eupelmus urozonus* (Deg.) ♀ (Eupelmidae). (3) Pro- and mesosternal regions of *Urocerus gigas* (L.) ♀ (Siricidae). 3*a*. Mesofurca, dorsal view. 3*b*. The same, seen from the right. (4) Mesosternal region of *Chrysis ignita* (L.) ♀ (Chrysididae). (5) *Priocnemis perturbator* (Harr.) ♀ (Pompilidae), pro- and mesothorax, seen from the left. (6) *Clytochrysus lapidarius* (Panz.) (*chrysostomus* Lep. and Br.) ♀ (Crabronidae), pro- and mesothorax seen from the left. (7) The fundamental plan of the hymenopterous mesosternum and mesopleuron.



FIGS. 1–7.—For explanation see opposite page.
Abbreviations, p. 104.

narrowly downwards to meet one another on the mid-ventral line in front of the spinasternum. The pronotum then takes the form of a complete ring, narrower below than above.

(4) *The trochantin and sternum of the second thoracic segment.*

The principal difficulty in applying Ferris's theory to the Hymenoptera appears when examining such primitive forms as *Macroxyela* (Ross, 1937, fig. 29) or *Xyela* (fig. 1). In these, the discriminal line is only developed on the posterior half of the ventral aspect of the mesothorax ; the anterior half where, if anywhere, pleural elements might be expected to meet on the mid-line shows no discrimen though there is a large membranous central area. In fact, in many Hymenoptera the discrimen extends only nearly but not quite to the anterior margin (e.g., *Prospaltella* (Aphelinidae), Snodgrass, 1910 : fig. 47), It seems that pleural elements are quite capable of fusing across the mid-ventral line without any external trace of it being visible in the adult. In some ways an even more diagrammatic mesosternum is seen in *Eupelmus* (Eupelmidae) (fig. 2), though the course of the pleural suture in this genus is very abnormal. In the Eupelmidae and the Encyrtidae, the mesepisternum is very large and the epimeron hidden beneath its posterior margin ; this arrangement may be connected with the development of the mid-legs for jumping.

It is here suggested that the triangular posterior area of *Xyela* and the rectangular plate of *Eupelmus* is in both cases the mesosternum. Although deeply invaginated along all or part of its mid-line, it is still quite broad. As in the prosternum, the furca (fig. 1, *a*) arises from a single central apophyseal pit. In most forms, the furca has a third backwardly directed arm, the spina, which in this case is fused to the segment in front, not to the one behind as in the prothorax. A narrow marginal area usually borders the ventral thoracic region posteriorly. In a species such as *Urocerus gigas* (L.) (Siricidae) (fig. 3), in which the mesosternum is much narrowed by invagination, the marginal area has all the appearance of a trochantin. It is suggested that the anterior margin of the mid coxal cavity includes, in most Hymenoptera, what is left of the trochantin. In some specialised types (e.g., *Arge cyaneocrocea* (Först.), Argidae), the trochantinal element seems to be very small. According to Arora (1952), both the mid and hind coxae are articulated at three points, to the pleuron, to the trochantin and to the sternum. Though the coxal condyles are often very little convex, their position is always indicated by a group of proprioreceptor sensilla.

In most Hymenoptera, the mesosternum is represented externally by the mid-ventral line along which it is invaginated and small posterior lobes between the mid coxae. The boundary between it and the pleuron is often uncertain.

(5) *The precoxal suture.*

Michener (1944) has elaborated a theory that the precoxal suture, instead of running from the edge of the mesosternum (represented in his scheme only by the apophyseal pit) to the lower part of the pleural suture, bends sharply forwards at the dorsal (or external) corner of the coxal cavity and runs, often partly obliterated, to near the dorsal anterior corner of the mesepisternum. Unfortunately, the exact course of such sutures is often difficult to make out and it seems at least equally plausible to suggest that the precoxal suture starts on the pleural suture, runs inwards and bends forwards at the point suggested by Michener. The part of Michener's precoxal suture nearest to the mid-line is, on this hypothesis, the anterior boundary of the trochantin. It seems after examining many genera that the precoxal suture normally ends at or near the anterior margin of the mesepisternum, not far from the mid-line. The suture which often connects the anterior end of the precoxal suture to the dorsal anterior corner of the mesepisternum is probably better regarded as a distinct epicnemial suture (Thomson, 1873, 1874) (= pre-episternal suture of Michener), defining an area known as the picnemium. Sometimes the precoxal and epicnemial sutures are almost continuous (*Cephus*, *Tiphia*) but they often cross or fail to meet. Michener has, I think correctly, recognised that the post-spiracular sclerite (or first parapterum) is enlarged in many Chalcids (and certain other families) and has been falsely identified with the epicnemium. It is probably in reality the anepisternum. Each area between the precoxal suture and the mid-ventral mesosternal line is a subpleural area (Michener) or precoxale. The two subpleural areas together with the mesosternum make up what taxonomists usually call the mesosternum.

Such a scheme is by no means easy to apply in practice, as is shown in the example of *Chrysis*. On the whole, the most likely interpretation seems to be the one indicated by the labelling of fig. 4, but it is difficult to prove that what have been called the precoxal sutures are not really the boundaries of the mesosternum and the " secondary carina ", not the precoxal suture. In many Chalcidoids (e.g. *Habrocytus trypetae* Thoms.) sutures not unlike those of *Eupelmus* seem really to be the precoxal sutures, the pleurosternal sutures being absent. The caution which Snodgrass (1935 : 171) has advocated in making such identifications seems well-justified, but it is probably convenient in any case to retain the term " mesosternum " whatever contributions from the pleuron or sternum may be involved. It may be noted that, while either the postspiracular sclerite or the epicnemium may be fused with its fellow across the mid-line, there is never any indication that this involves part of the mesosternum, so that Snodgrass's term " prepectus " seems inadvisable in this group. It is by no means easy in some groups to decide whether a sclerite is a postspiracular sclerite or an epicnemium when only one of these is present.

The picture may be further complicated by secondary sutures (or carinae). Two, in particular, seem of importance in higher Hymenoptera. First, one which runs in such families as the Pompilidae (fig. 5) and some Dryinidae from near the ventral end of the epicnemial suture to the mesepisternal scrobe, dividing the mesepisternum into a smaller dorsal and larger ventral part. This is the *posterior oblique suture*. The second runs up from about the same point to the subalar pit in many Sphecoids and bees. It has usually been identified as the epicnemial (prepectal, pre-episternal) suture but it seems from an examination of such forms as *Clytochrysus* (fig. 6) or *Prosopis*, in which both are present that it is a new structure tending to replace the original epicnemial suture. This *anterior oblique suture* defines an anterior division of the mesepisternum which has been called the " prepectus ". Fig. 7 shows the general plan of all these structures.

(6) *The metasternum.*

It is less necessary for taxonomic purposes to be able to homologise the parts of the plate lying behind the mid and in front of the hind coxae. On grounds of analogy one would expect it to consist of the metasternum and third trochantin. In *Trypoxylon* subpleural areas seem to be marked off ; in *Sphex* the meso- and metasternum are fused together. For descriptive purposes, the term metasternum is probably unobjectionable.

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Abbreviations.

The numbers 1 or 2 refer to the first or second thoracic segment. *A.o.s.*, anterior oblique suture. *Bsl.*, basalare. *Ce. scl.*, cervical sclerite. *Epc.*, epicnemium. *Epm.*, epimeron. *Eps.*, episternum. *N.*, notum. *Pl.*, pleuron. *Pl.s.*, pleural suture. *P.o.s.*, posterior oblique suture. *Prcx. s.*, precoxal suture. *Psp. scl.*, postspiracular sclerite. *Sbl.*, subalare. *Sbl. pit*, subalar pit. *Sc.*, scutum. *Scl.*, scutellum. *Scr.*, mesepisternal scrobe. *Sp.*, peritreme of spiracle. *Spl. a.*, subpleural area (precoxale). *Spn.*, spina. *St.*, sternum. *Tg.*, tegula. *Trn.*, trochantin.

THE TRACHEAL SYSTEM OF THE LARVA OF *LONCHOPTERA LUTEA* PANZER (DIPTERA: LONCHOPTERIDAE).

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Introduction.

The larva of *Lonchoptera*, the only genus of the family Lonchopteridae, was described in 1900 by de Meijere. The larvae of this genus are unlike any other dipterous larva : they are flattened ventrally and arched dorsally, the dorsal surface of the segments being so chitinised as to give the appearance of a number of shields. Each of these has the lateral and posterior margins deeply serrated. The first segment to be chitinised dorsally is the meso-thoracic, on which the serrations are on the anterior border only. The mature third instar larva found recently by the author is that of *Lonchoptera lutea* Panzer. It is distinguishable from the larva of *Lonchoptera furcata* Fallén by the numbers of marginal serrations between the anal filaments and between the inner mesothoracic filaments, by the relative lengths of the inner and outer mesothoracic filaments and by the length of the last pair of marginal papillae.

The head and prothorax are retracted ; the visible segments number eight, but it was thought by de Meijere (1900) that the second dorsally chitinised segment is the metathoracic and first abdominal combined, and Lundbeck (1916) further suggests that the last may similarly represent two segments, so arriving at the normal number of twelve segments.

The tracheal system was described by de Meijere (1900), but during a recent comparative study, by the present author, of the larval tracheal system in the Diptera (Whitten, 1955) it was found that his description was too incomplete for detailed comparison with other Diptera. The tracheal system was shown by de Meijere (1900) to be amphipneustic, with first-thoracic and last abdominal spiracles functional. The dorsal longitudinal trunks were connected, in his figures, by only nine dorsal commissures, and the lateral and dorsal trunks of either side were joined by only seven transverse connectives, whereas in other Diptera there are ten dorsal anastomoses and eight transverse connectives. Moreover, the anterior end was incompletely figured by de Meijere, and details of the tracheae to the ventral nerve mass were not given.

When the results of the investigation of the larval Diptera were submitted for publication, de Meijere's (1900) description was the only available source of information on the tracheal system of this family. It is only since the submission of the former paper that the present larva has been found and studied.

The Larval Tracheal System.

As was shown by de Meijere (1900), the larva is amphipneustic. The first pair of spiracles lie at the apex of a short prothoracic papilla, and the last pair lie lateral to the long anal filaments. The last pair of spiracles are placed widely apart.

Dorsal longitudinal trunks (*d.l.t.*).—This pair of trunks passes backwards in almost a straight line from the first to last pair of spiracles. They are slightly farther apart posteriorly, due to the relative positions of the spiracles.

Lateral longitudinal trunks (*l.l.t.*).—These trunks are wider apart than are the dorsal, but likewise extend the length of the larva. They join the dorsal trunks of either side at the extreme anterior and posterior ends.

Dorsal anastomoses (*commissures*) (*d.a.*).—The dorsal trunks are connected by ten tracheae, and not nine as described by de Meijere (1900). The first and last of these resemble those of other Cyclorrhapha in being wider in diameter than are numbers two to nine inclusive. The first two are difficult to see owing to the retractibility of the anterior end and the opaque nature of the succeeding region. The second of these anastomoses was not observed by de Meijere; had it been, his total complement would also have been ten.

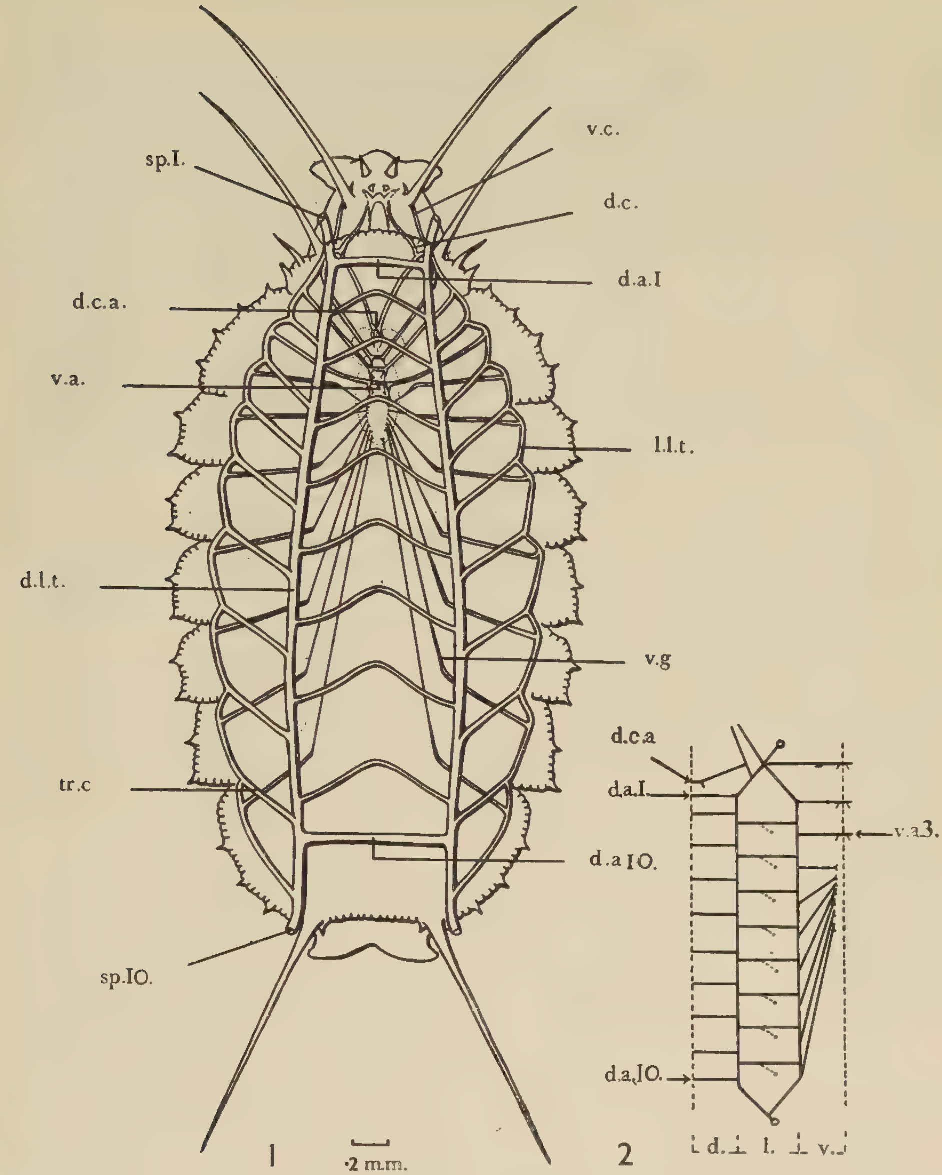
Transverse connectives (*tr.c.*).—The dorsal and lateral trunks, beside their union anteriorly and posteriorly, are connected by eight tracheae—the transverse connectives; de Meijere's total number of seven appears to be due to confusion at the anterior end, again probably due to opacity in this region. The first transverse connective arises from the dorsal trunk posterior to the second dorsal anastomosis; the second to tenth arise between respective dorsal anastomoses and the last pair of spiracles.

Spiracular tracheae.—Those of the first and last are long and well-developed; those of the non-functional spiracles are collapsed and form solid cords (Palmén's (1877) threads) arising one from each of the transverse connectives.

Ventral cervical tracheae (*v.c.*).—Arising at the junction on either side of the lateral and dorsal trunks with the spiracular tracheae of the first pair of spiracles, is a trachea which passes anteriorly to the region of the mouth armature; this is the ventral cervical trachea. As will be described later, it gives rise to the first trachea which passes to the ventral nerve mass.

Dorsal cervical tracheae (*d.c.*).—These arise from the dorsal trunks immediately posterior to the junction of these trunks with the lateral trunks. Each immediately divides into two; one part passes anteriorly to the region of the mouth armature; the other passes posteriorly and medially. At the level of the supra-oesophageal ganglia it divides, the medianly directed branch anastomosing with its fellow, while the other branch passes to the "brain". The anastomosis corresponds to the *dorsal cervical anastomosis* (*d.c.a.*) of other Diptera.

Ventral ganglionic tracheae (*v.g.*).—The ventral nerve mass, formed from fused nerve ganglia, is tracheated by tracheae arising from the ventral cervical tracheae and longitudinal trunks. The first pair arises from the ventral cervical tracheae near their points of origin. The second pair arises from the lateral trunks posterior to their origin, and the third to ninth pairs arise from the trunks slightly posterior to the junction of these with the respective transverse connectives. Due to the concentration of the nervous system, the tracheae arising from the posterior tracheal segments traverse the abdomen in order to tracheate the nerve mass. The first three pairs of tracheae correspond to the pro-, meso- and metathoracic ganglionic tracheae of more generalised Diptera, and, likewise, form mid-ventral anastomoses (*v.a.*). The latter are not formed by the abdominal tracheae. The second and third ventral anastomoses are not shown by de Meijere (1900).



FIGS. 1–2.—*Lonchoptera lutea* Panzer. (1) Larval tracheal system in dorsal view. (2) Plan of right half of larval system.

CONCLUSIONS.

The main tracheae constitute the same fundamental tracheal pattern as has been shown for other Diptera (Whitten, 1955). The curious external appearance, therefore, is not accompanied by any anomalies in the tracheal system. On the contrary, de Meijere's (1900) description for *Lonchoptera* presented a tracheal system which appeared anomalous when comparisons were made with other dipterous larval systems. Reinvestigation of the system reveals important omissions in de Meijere's description. The tracheal pattern, instead of being anomalous, confirms a previously expressed opinion of the author that a generalised dipterous larval pattern, constant for many Nematocera, Brachycera and practically all Cyclorrhapha, is present in the Diptera.

The system of *Lonchoptera* resembles, in detail, that of the Diptera Cyclorrhapha. This sub-order is characterised by the positions of origin of the dorsal and ventral cervical tracheae and of the first ventral ganglionic tracheae, in relation to the anterior junctions of the dorsal and lateral longitudinal trunks. Further, the positions of the dorsal cervical anastomosis and of the anteriorly displaced abdominal ventral ganglionic tracheae are characteristic of, but not confined to, the Diptera Cyclorrhapha.

The metameric pattern of the tracheal system substantiates de Meijere's (1900) opinion that the number of body segments is normal, the metathoracic chitinized region representing two segments, as also does the last chitinised region.

SUMMARY.

The tracheal system of the larva of *Lonchoptera lutea* Panzer is described. The pattern formed by the main elements is shown to agree closely with that of the Diptera Cyclorrhapha. The number of body segments suggested by the form of the tracheal system is twelve.

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THE MEDIAN FACIAL SCLERITE IN LARVAL AND ADULT LEPIDOPTERA.

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I. Introduction.

This paper is an attempt to interpret the morphology of the triangular median sclerite in the face of caterpillars and the corresponding quadrangular sclerite in that of adult Lepidoptera in the light of recent additions to our knowledge of the morphology of the insect head. This new knowledge includes the recognition of (1) the nature of the frontogenal inflections; (2) the occurrence of clypeogenal inflections in the heads of some specialised insects; (3) the primitive position of the anterior tentorial pits in the ventral extremities of the frontogenal sutures at the level of the morphological mouth; (4) the fact that the frontal ganglion, which develops immediately behind the morphological mouth, retains this position regardless of changes in the structure of the head.

The older criteria based on the origin of the facial muscles are also employed and their validity discussed.

The interpretations given are based on the definition of the clypeus as a preoral, and of the frons as a postoral, sclerite.

II. The Larva.

Older interpretations

The most striking feature in the face of caterpillars is a deep inverted Y-shaped inflection which consists proximally of a mid-cranial ridge and distally of two diverging arms which run obliquely to the neighbourhood of the anterior mandibular articulations. Externally the two arms form an inverted V-shaped sulcus which embraces two sides of the triangular median sclerite with which we are here concerned. The anterior tentorial pits lie in this sulcus near the middle of its arms.

A line suture or cleavage line runs along each inturned edge of the mid-cranial inflection, but before the latter branches the cleavage lines leave it and run obliquely down the face lateral to the arms of the V-shaped sulcus.

In the older literature the Y-shaped sulcus was interpreted as the "epicranial suture" and the triangular sclerite as the frons. The cleavage lines were known as adfrontal sutures and the narrow sclerites between them and the triangular plate were known as adfrontal sclerites.

Snodgrass (1928) recognised that the cleavage lines are the equivalent of the frontal suture in other insects and claimed, therefore, that the "adfrontals" are parts of the frons, the remainder of the frons being inflected to form the midcranial ridge. He interprets the V-shaped sulcus as the frontoclypeal suture because of his contention that the tentorial pits invariably lie in this suture. He believed the suture to have arched upwards, encroaching on the frontal region. The triangular sclerite would, therefore, be the clypeus or, at least, the post-clypeus. He showed further that the cibarial muscles originate in this sclerite.

Recognising that the tentorial pits lie primitively in the frontogenal sutures and only rarely migrate to the frontoclypeal, DuPorte (1946) interpreted the distal portions of the sulci, including the tentorial pits, as frontogenal sutures and suggested that the proximal portion might be a transfrontal suture. On this interpretation the median plate would be an antefrons.

Hinton (1948) does not accept either of these interpretations. He points out that two pairs of precerebral pharyngeal dilators originate on the sclerite in addition to the cibarial muscles ; therefore, the sclerite must in part belong to the frons. A third pair of pharyngeal dilators originate in the cranial wall lateral to the cleavage lines and he believes their point of origin is part of the frons. He comes to the essentially correct conclusion that the triangular sclerite is a clypeofrontal sclerite, but claims that it is neither the entire frons nor the entire clypeus. Apparently he believes that the V-shaped sulcus, which he calls the adfrontal sutures, is unrelated to the normal sulci of generalized insects and that it cuts through both frons and clypeus.

Short (1951) examined Hinton's criticism of Snodgrass' views and concluded that " the importance of the deviations from Snodgrass' generalisations which occur in the caterpillar head cannot be estimated without further detailed study into other groups. Present evidence indicates that these generalisations are substantially correct ".

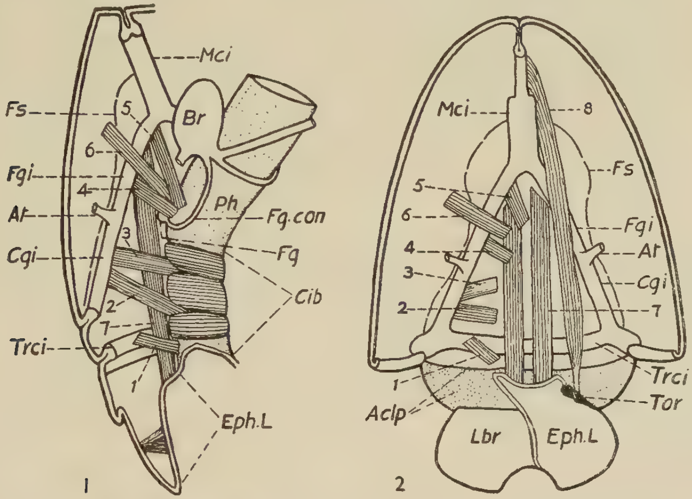
Snodgrass (1935) defines the clypeus as the region from which the cibarial muscles originate. This criterion is useless unless the boundary between the cibarium and the pharynx can be recognised and this is not always possible. Later (1947), however, he gave a criterion for recognising the position of the primary mouth and therefore for distinguishing between the pharynx and the cibarium. In the embryo the frontal ganglion develops immediately behind the mouth and Snodgrass has shown, on good evidence, that it retains this position regardless of the changes that might take place in the structure of the head. The dorsal cibarial dilators, according to him, originate in the clypeus and are inserted in the foregut ventral (or anterior) to the frontal ganglion. The precerebral pharyngeal dilators, as well as the labral muscles, originate in the frons and the former are inserted in the pharynx within the loops formed by the frontal ganglion connectives.

A new interpretation.

In an earlier contribution (DuPorte, 1946), I drew attention to the morphological importance of the frontogenal sutures which are formed between the median, ventrally projecting sclerite of the face and the lateral or genal regions when the latter descend ventrally to the level of the mouth. The anterior tentorial pits are located primitively in the ventral ends of these sutures at the level of the mouth and not in the frontoclypeal suture, though they occasionally migrate into this. It was not realised at the time that in many higher insects the ventral descent of the genal regions continues beyond the level of the mouth and that, as a consequence, a pair of clypeogenal sutures is formed between the clypeus and the genae (DuPorte and Bigelow, 1952). Consequently the sutures which in some insects I interpreted as the frontogenal are really the clypeogenal or the two combined. Since these sutures are continuous and formed as the result of the same developmental process, the two combined may be termed the *laterofacial suture.*

In the Hymenoptera the tentorial pits retain their position at the level of the primary mouth in spite of the changes which have taken place in the face (DuPorte and Bigelow, 1952 ; Bigelow, 1954). Their position may therefore be taken as an additional criterion, though not an infallible one, of the dividing line between the frons and the clypeus.

With this new information on the morphology of the face, in addition to Snodgrass' criteria, it should be possible to reach an acceptable interpretation of the nature of the median sclerite.



FIGS. 1–2.—*Protoparce quinquemaculata* Haworth. Larva. (1) Lateral view of internal head structures. (2) Facial region, internal view.

The observations recorded here were made chiefly on the larva of the sphingid *Protoparce quinquemaculata* (Haworth). Because of the homogeneity in structure of the head in caterpillars, no attempt was made to study a long series, though checks were made on several other species. Besides, the anatomical features, though not their interpretation, agree very closely with those recorded by Snodgrass, Hinton and Short.

In all species examined the frontal ganglion (fig. 1, *Fg*) and the base of the anterior tentorial arms (*At*) are approximately at the same level. There is thus double evidence for the location of the primary mouth at this level, and a line drawn between the tentorial pits would indicate the position of the frontoclypeal suture if this were developed. The region of the median sclerite ventral to the tentorial pits may, therefore, be referred to as the clypeal region and that dorsal to the pits as the frontal region.

Two pairs of pharyngeal dilators (figs. 1 and 2, *4*, *5*) originate in the frontal region. These, with a third pair (*6*), which originates in the cranial wall lateral to the cleavage lines (figs. 1 and 2, *Fs*) are inserted in the pharynx within the loops formed by the frontal ganglion connectives (fig. 1, *Fg. con*). These muscles, by Snodgrass' criterion, originate in the frons.

Three pairs of cibarial dilators (figs. 1 and 2, *1*, *2*, *3*) originate in the clypeal region and are inserted in the foregut ventral to the frontal ganglion. These by Snodgrass' criterion originate in the clypeus.

Another pair of muscles (figs. 1 and 2, *7*) originates near the apex of the frontal region of the sclerite. Snodgrass, Hinton and Short describe these as cibarial muscles. By Snodgrass' criterion these, of course, should originate in the clypeus. In *Protoparce* these muscles are inserted ventral to the first constrictor of the cibarium and their point of insertion I believe to be, not the cibarium, but the median region of the inner or epipharyngeal wall of the labrum (figs. 1 and 2, *Eph. L*). Their contraction can have little effect on the cibarium, but does retract the labrum, as can be readily demonstrated by pulling on them with the forceps. It is true that their insertion is dorsal to the level of the clypeolabral suture, but so is that of the lateral retractors (fig. 2, *8*) inserted in the tormae. It will be observed that the tormae (fig. 2, *Tor*) are not horizontal but run obliquely in such a way as to suggest that the inner wall of the labrum extends further dorsally than the outer wall. If the interpretation of these muscles as labral muscles is correct their origin from the frontal region of the sclerite is normal.

All the evidence therefore—the position of the frontal ganglion and the tentorial arms, and the origin of the pharyngeal, cibarial and labral muscles—indicates that the region of the sclerite ventral to the tentorial pits pertains to the clypeus, while that dorsal to the pits pertains to the frons. If we regard the frons as a definite area between the frontogenal sutures (DuPorte, 1946) then the apical half of the sclerite is the entire frons. If we regard it as an indefinite region dorsal to the clypeus (Snodgrass, 1947) then this region is only part of the frons.

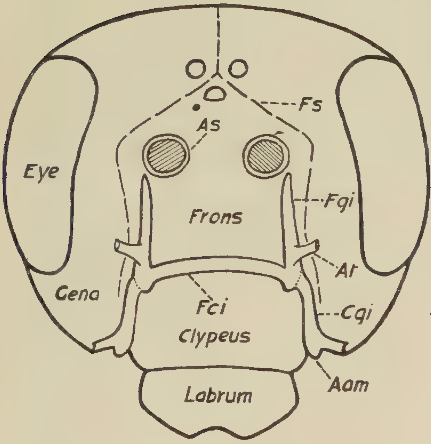
If the interpretation of the sclerite given here is correct there is no frontoclypeal inflection. The arms of the V are laterofacial inflections, each consisting of a frontogenal inflection (figs. 1 and 2, *Fgi*) with the tentorial arms attached at its lower end, and a clypeogenal inflection (*Cgi*). In *Protoparce*, but not in all caterpillars, there is a submarginal transclypeal inflection (*Trci*) which cuts off a narrow ventral sclerite. This sclerite, with the membranous area that follows, may be regarded as the anteclypeus (fig. 2, *Aclp*).

Fig. 3 is a schematic representation of the inner surface of the face in some of the higher insects according to the theory of DuPorte and Bigelow (1952). The cleavage line is absent in the adult head but is shown here for comparison. The compound eyes and dorsal ocelli are of course lacking in the caterpillar and the position of the antennae is different, but allowing for these differences, it will be seen that if a median inflection occurred in the vertex, deep enough to bring the ends of the frontogenal inflections together, and if the frontoclypeal inflection disappeared, the result would be to produce a facial aspect exactly like that of a caterpillar.

III. The Adult.

The head structures in the adult are more variable than those in the larva. The median facial sclerite is roughly quadrangular in form. It is bounded laterally by two vertical sutures (fig. 5, *Lfs*) which extend from the clypeolabral suture dorsally to the lateral edges of the antennal sockets, and dorsally by a transverse suture (*Trfs*) extending between the sockets. The inflections with which the vertical sutures are associated unite with the antennal ridges; therefore the transverse suture might be regarded as uniting the dorsal ends of the vertical ones.

The only important external variation in this facial structure lies in the position of the tentorial pits. At one extreme they lie high up in the vertical sutures, at the other they lie in the ventral ends of the sutures at their junction with the clypeolabral suture. The two heads to be described differ externally in the position of the tentorial pits and internally in the origin of the cibarial and pharyngeal muscles.



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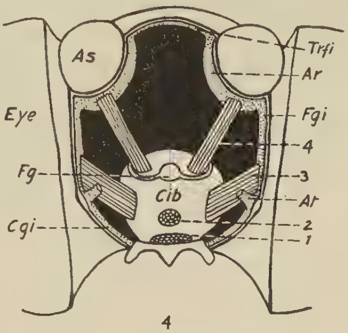

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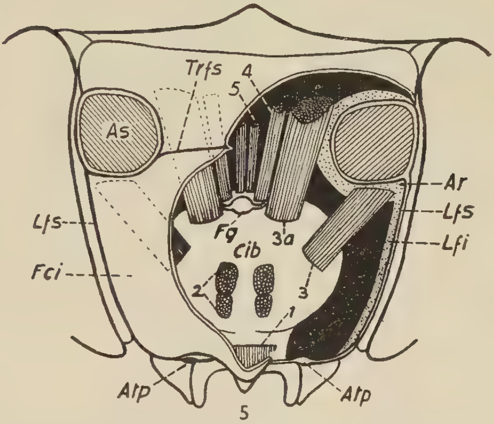

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Figs. 3–5.—(3) Typical internal facial structure of some higher insects. (Ecdysial suture added.) (4) *Danaus plexippus* L. Adult. Anterior view of head with frontoclypeal sclerite removed. (5) *P. quinquemaculata* Haworth. Adult. Anterior view of head with part of facial sclerites removed.

Danaus plexippus (Linn.).

In *Danaus* (fig. 4) the tentorial pits lie some distance dorsal to the ventral extremity of the vertical sutures. The sucking pump (*Cib*), which is apparently formed chiefly from the cibarium with some contribution from the pharynx, is relatively enormous in size compared with that portion of the pharynx which follows it. The large dorsal bulge of the pump must cause some changes in the relative positions of the structures associated with it. The frontal ganglion connectives, for example, extend anteriorly from the brain instead of ventrally and this probably displaces the ganglion dorsally so that its primitive position in relation to the tentorial arms is difficult to determine. The position of the mouth, however, as determined by the position of the ganglion, lies a considerable distance ventral to the transverse inflection (fig. 4, *Trfi*). Therefore the latter cannot be the frontoclypeal inflection.

A pair of precerebral pharyngeal dilators (fig. 4, *4*) originate in the antennal ridges and are inserted within the loops formed by the frontal ganglion connectives. This suggests that the dorsal portion of the sclerite belongs to the frons.

There are two median dilators of the cibarium. One (fig. 4, *1*) originates near the ventral edge of the facial sclerite and is inserted dorsal to the secondary mouth. The second (fig. 4, *2*) originates dorsal to the first, but both originate ventral to a line drawn between the tentorial arms, therefore, presumably from the clypeal region. A third and very strong paired muscle (fig. 4, *3*) originates from the lateral inflections immediately dorsal to the tentorial arms and is inserted in the cibarium ventral to the arms. It may be presumed that these are cibarial muscles which have shifted their origin to the frontal region to increase their mechanical efficiency, but the possibility of a ventral shift in the position of the tentorial arms cannot be ignored.

On the whole there is an essential similarity between the facial sclerite in the adult *Danaus* and in caterpillars and it seems reasonable to interpret the sclerite in the adult as a frontoclypeal sclerite and not merely as the clypeus. The vertical sutures would then be laterofacial sutures. Earlier (DuPorte, 1946) they were interpreted as frontogenal sutures but obviously the clypeogenal sutures also enter into their composition. The transverse suture may be termed the transfrontal suture.

Reference to fig. 3 will show that, if the frontoclypeal suture disappears and a transfrontal suture unites the dorsal ends of the laterofacials, the structure of the face will be essentially as in *Danaus*.

Protoparce quinquemaculata Haworth.

The three criteria used define the clypeus and frons in *Danaus* almost as decisively as in the larval head, but in *Protoparce* two of these criteria fail. The tentorial pits lie at the level of the secondary mouth ; therefore, all of the cibarial muscles originate dorsal to the pits.

The muscles of the sucking pump are stronger and more numerous than those of *Danaus*. This is probably correlated with the long proboscis of the sphinx moth and the need for more powerful suction. Two of these muscles (fig. 5, *1* & *2*) are obviously the homologues of the correspondingly numbered muscles in *Danaus*. Muscles 3 in the two insects are also probably homologous, but in *Protoparce* they originate in the antennal ridges, in the same position as do the pharyngeal muscles in *Danaus*.

An additional pair of muscles (fig. 5, *3a*), not represented in *Danaus*, originates outside the facial sclerite and far dorsal to it. It would require a considerable stretch of the imagination to interpret the region of their origin as part of the clypeus. Besides, one pair of pharyngeal dilators (fig. 5, *4*) originates at the same level and a second pair (5) actually ventral to this level.

There are two alternative interpretations of the conditions found in *Protoparce*. One is that the tentorial pits have retained their position at the level of the morphological mouth, which implies that the genal regions in this insect have not descended beyond the level of the mouth. On this interpretation the trilobed sclerite, commonly recognised as the labrum, would be the reduced clypeus. It would have to be assumed that the cibarium retained its normal length and was forced into the frontal region as the result of the reduction in the clypeus and, for the same reason, the origin of the cibarial muscles was shifted to the frons. This, in effect, was the interpretation given earlier by me (DuPorte, 1946).

In the light of recent knowledge the second alternative is more acceptable. The tentorial pits have apparently migrated ventrally in the clypeogenal sutures and no longer mark the dividing line between the clypeus and frons, but, as in *Danaus*, the median sclerite is still a frontoclypeal sclerite.

The anomalies in the origin of the dilator muscles remain to be explained. Snodgrass (1947) has proposed two generalisations concerning the points of origin of the facial muscles. One is that the frontal sutures invariably pass between the facial muscles and the muscles of the mandibles and maxillae. The other is that the dorsal dilators of the cibarium originate in the clypeus, while those of the pharynx originate in the frons. My own observations and those of others confirm the soundness of both as generalisations, but the possibility of exceptions must be recognised. Muscles are purely functional units and their mechanical efficiency depends in large part on their point of origin in the skeleton. With changes in the form or in the direction of growth of the organs they move they must often shift their origins even if this involves crossing a secondary inflection. Indeed they sometimes cross primary intersegmental lines. The head of the caterpillar offers an exception to the first generalisation, since a pair of pharyngeal muscles originates lateral to the frontal suture and a few strands of the mandibular adductors originate from the midcranial inflection which is mesal to this suture. A clear exception to the second generalisation is provided by the adult *Protoparce*. While two sets of cibarial muscles originate from what is obviously the clypeal region, one pair originates from what is probably the frons but could be interpreted as the clypeus, and another pair originates from an area which cannot be interpreted as the clypeus.

While, therefore, the origin of the muscles is an important aid in determining the identity of sclerites, it is not an infallible one and due weight must be given to conflicting evidence from other sources.

IV. SUMMARY.

1. The triangular median facial sclerite of the caterpillar is interpreted as being composed of the postclypeus plus the frons, or at least part of the frontal region, on the following evidence :

   (a) The frontal ganglion and the tentorial pits lie at the same level and mark the position of the primary mouth ; therefore, a line drawn between the tentorial pits divides the sclerite into a postoral frontal region and a preoral clypeal region.

(b) The cibarial dilators originate in the clypeal region while the pharyngeal dilators originate in the frontal region.

2. There is no frontoclypeal suture. The oblique sutures lateral to the frontoclypeal sclerite in the caterpillar are laterofacial sutures whose dorsal extremities are drawn together as the result of the deep midcranial inflection.

3. The median quadrangular sclerite of the adult face also is a frontoclypeal sclerite bounded laterally by laterofacial sutures and dorsally by a transfrontal suture.

4. The arrangement of the facial muscles in the adult *Danaus* is essentially similar to that in caterpillars.

5. In the adult *Protoparce* the tentorial pits have migrated ventrally in the clypeogenal sutures and the cibarial muscles originate dorsal to the tentorial arms. One pair originates dorsal to the frontoclypeal sclerite in a region which cannot be interpreted as the clypeus. The pharyngeal dilators originate in the same region.

6. The facial muscles in both larva and adult provide exceptions to Snodgrass' generalisations on the value of these muscles in interpreting the facial regions or sclerites.

Abbreviations

Aam., anterior mandibular articulation.
Aclp., anteclypeus.
Ar., antennal ridge.
At., anterior tentorial arm.
Atp., anterior tentorial pit.
Br., Brain.
Cgi., clypeogenal inflection.
Cib., cibarium.
Eph.L., epipharyngeal lining of labrum.
Fcl., frontoclypeal sclerite.
Fg., frontal ganglion.
Fg. con., frontal ganglion connective.
Fgi., frontogenal inflection.
Fs., frontal suture.
Lbr., labrum.
Lfs., laterofacial sulcus.
Lfi., laterofacial inflection.
Mci., midcranial inflection.
Ph., Pharynx.
Tor., torma.
Trci., transclypeal inflection.
Trfs., transfrontal suture.
1, 2, 3, 3a, dorsal dilators of cibarium.
4, 5, 6, dorsal dilators of pharynx.
7, Inner retractors of labrum.
8, outer retractors of labrum.

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OBSERVATIONS ON THE BIOLOGY OF SOME AGROMYZIDAE (DIPTERA).

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The life cycles of only a few individual species of Agromyzidae have been studied. The major works on morphology (Hering, 1927; Hendel, 1931–36) and hypnomology[1] (Hering, 1937) refer to dates when the flies may be found, but biological information is very brief. Séguy (1934) gives some records of parasites, but this aspect, too, has been much neglected. All these authors are concerned with conditions on the continent of Europe. The present notes fill some of the gaps in our knowledge of the position in Britain.

Only species living on plants of the family Umbelliferae were considered, and all observations were made in the Sunninghill area of Berkshire.

Biology.

The larval stadia are spent in mining plant tissues, and there are three instars, followed by a pupal instar, within the mine in some species but not in others. All the leaf mining species studied here pupate externally, but the stem miners *in situ.*

The male fly seems to feed on nectar and the female on plant sap, which she obtains by making punctures in the leaf surface with her ovipostor and feeding on the exudate. Similar punctures are made for oviposition, but the ovipositor is extended further into the leaf tissue before the egg is laid. Oviposition by stem mining species was not observed, but is probably very much the same.

Rearing Methods.

No successful method was found to cause flies reared in the laboratory to lay eggs, but flies captured in the field would often do so. It was sufficient to introduce a leaf, or part of a leaf, into a specimen tube containing the female fly.

To find the lengths of larval stadia in leaf mining species, infected leaves were kept with their stems in water, and the advancing end of the mine was marked each day with a different colour of paint. Artists' water-colour paint was used, being adequate for the purpose, and less likely to affect the underlying larva than a paint with an oily base. After emergence of the larva for pupation the mine was opened, and the position of the larval exuviae indicated the dates of ecdysis, and hence the lengths of the stadia. In species which had an "initial mine", in which the under part of the leaf tissue, and not the palisade parenchyma, was attacked, it was possible to find the proportion of the stadium spent in this part.

Pupae were kept in corked specimen tubes, which treatment seemed sufficient to prevent dehydration over quite long periods. It was found that if moist cotton wool, or filter paper, were kept in the tubes, the condensation on the glass tube spoiled the newly emerged adults, which were nearly always trapped by it, and there was also a tendency for mould to form.

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[1] Derived from ὑπόνομος = a mine, λόγος = the study of.—Editor.

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Napomyza lateralis (Fallén).

Host plants.—There are records of mines from the following plants :

Compositae.—Receptacles of *Anthemis arvensis* L., *A. cotula* L., *Bidens cernuus* L., *Centaurea jacea* L., *C. nigra* L., *Cichorium intybus* L., *Helianthus tuberosus* L., *Inula britannica* L., *Matricaria chamomilla* L., *M. maritima* ssp. *inodora* L., *Senecio aquaticus* L., *S. vulgaris* L., Leaves of *Bellis perennis* L., *Cichorium endivia* L., *Crepis capillaris* Wallr., *Hypochoeris glabra* L. Stems of *Chrysanthemum segetum* L., *Stachys germanica* L.

Labiatae.—*Verbena officinalis* L.

Ranunculaceae.—*Clematis* sp.

Scrophulariaceae.—*Digitalis purpurea* L., *Odontites verna* Dum.

Urticaceae.—*Urtica dioica* L.

Umbelliferae.—Stems and petioles of *Anthriscus sylvestris* (L.) Bernh. Petioles of *Daucus carota* L.

To the above I would add stems of *Aegopodium podagraria* L., *Conopodium majus* (Gouan) Lor. and Barr, and *Torilis japonica* (Houtt.) DC.

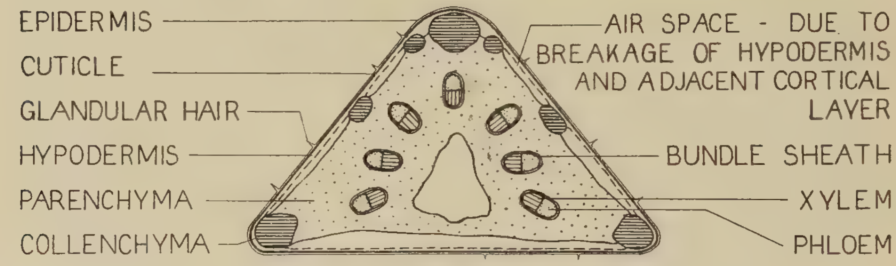

Fig. 1.—Transverse section of petiole of *Anthriscus sylvestris.*

Mine.—It was found impossible to trace the course of the mine in the stem, all but the broadest, final portion being invisible. Mining seems to be always in the main part of the stem, not in the side branches, and pupation is usually at the base. In the leaves, mining is mainly in the broadest part of the petiole, and successive petioles are mined, the larva moving inward to the centre from the outside leaves of the rosette. The mines can be detected as brownish streaks on the otherwise white petiole, and callus tissue can often be found in them. They usually run straight up and down, between the vascular bundles and parallel with them. Although the larva can move from a mine in one petiole to mine another, closely pressed against the first, it does not seem able to penetrate the surface if removed from the mine. It can, however, be transferred to another leaf if a short space is excavated for it, and will usually continue this artificial mine quite satisfactorily.

Pupation in the petiole takes place higher up than the normal mine extends, and the pupa lies head upward, as in fig. 2. A small part of the parenchyma in front of it is removed, and part of the hypodermis, so that the emerging adult must only break through a " window " of epidermis and cuticle.

Period of occurrence.—Hendel (1931–36) and van den Bruel (1933) take the pupa to be the normal overwintering stage. Hering (1927) states that the imago normally overwinters, but that in Umbellifer stems the pupa may do so.

De Meijere mentions pupae in the stems in winter, but states that he obtained no adult flies from them, for they were mostly empty or parasitized.

Table I shows the stage of development of material examined at different times of the year. From it the following life cycle seems evident, though slightly at variance with the opinions quoted above :

Table I.—*Period of Occurrence of* Napomyza lateralis *Fallén on* A. sylvestris.

	Month.																							
	I.		II.		III.		IV.		V.		VI.		VII.		VIII.		IX.		X.		XI.		XII.	
Larva in petiole	+	.	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pupa in ,,	.	.	.	+±	+±	+±	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Adult in ,,	.	.	.	.	.	±	.	±	+	+	.	.	.	.	±	±	±	.	.	.	.	.	.	.
Larva in stem	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Pupa in ,,	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	+	.	.	+	.	.	.	.	.

+ = material found in the field.
± = material reared in laboratory.

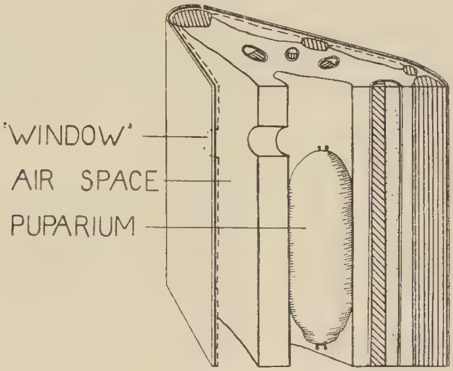

Fig. 2.—Longitudinal section of petiole of *Anthriscus sylvestris*, with puparium of *N. lateralis*.

Flies emerging in April and May lay eggs in the stems of *Anthriscus sylvestris*. Larvae from these eggs mine in the pithy stem and pupate in July and August, emerging in August and September. The stems are by this time dead and withered, so that the eggs of the next generation are laid in the new leaves, which are now appearing. Larvae mine the petioles and pupate the following February, March, and April. It is impossible to find very young larvae in either petioles or stems, but their presence must be assumed in June and December.

Lengths of stadia.—It was not possible to study the lengths of larval stadia in the same detail as for leaf miners, since the presence of miners in the stem or petiole is not visible externally. Nevertheless, if a period of about a month or longer is allowed in the life cycle for the maturation of eggs in the adult, the larval life up to the time of pupation would occupy something in the region of at least two months.

The period of pupation for winter larvae reared in laboratory conditions is given by van den Bruel as 38–44 days. Pupae reared by me emerged in 19–27 days in March and April, and about 38 days in August.

Parasitism.—Of 34 pupae reared from winter larvae, 9 adult flies emerged, and 3 *Dacnusa senilis* (Nees) (Braconidae). Of the unemerged pupae 3 would also have yielded *Dacnusa.*

Of 36 pupae reared from summer larvae, 7 adults emerged, 8 *Dacnusa senilis*, 3 *Sphegigaster* sp. (Pteromalidae), and one other Chalcid. Of the remainder, 1 would have given a *D. senilis*, and there were still 2 living hymenopteran larvae when the pupae were opened in January.

If it is assumed that all the pupae would have emerged had they been under natural conditions, we find a parasitism in the winter generation in the order of 18 per cent., or, in the summer, of 42—(25 per cent. due to *D. senilis*, and 17 per cent. due to chalcids). It would appear that the chalcids may not attack the winter generation, but may overwinter in the stems, only emerging the following spring.

In the winter larvae the percentage parasitism of those emerging was 25 per cent., and of the unemerged 14 per cent. For the summer larvae the figures are 63 per cent. and 18 per-cent. These indicate a relatively greater emergence of parasites than of their hosts, and it would seem that the parasites must be less affected by the unnatural conditions of the laboratory than are the hosts, if, as seems probable, these conditions are responsible for the mortality.

A few cocoons of *Stenomalus muscarum* (L.) (Pteromalidae) were found in *Anthriscus sylvestris* and *Torilis japonica* stems. This was thought to be a parasite on the larval stages of *N. lateralis.*

Van den Bruel records the parasites of this species as *Dacnusa leptogaster* Hal., *Stenomalus muscarum* (L.), and *Sphegigaster* sp. Séguy records *Dacnusa flavipes* Gour. and *Entedon gracilis* Gour., both non-British species.

Melanagromyza aeneiventris (Fallén).

Host plants.—Recorded from:

Compositae.—Leaves and stems of *Arctium lappa* L., stems of *Aster tripolium* L., *Carduus nutans* L., *Centaurea jacea* L., *Cirsium arvense* Scop., *C. eriophorum* Scop., *C. vulgare* Ten., *Eupatorium cannabinum* L., *Helianthus tuberosus* L., *Senecio aquaticus* Hill.

Urticaceae.—Leaves and stems of *Urtica dioica* L.

Crassulaceae.—Leaves of *Sedum telephium* L.

Umbelliferae.—I add stems of *Heracleum sphondylium* L., *Pastinaca sativa* L., *Torilis japonica* (Houtt.) DC.

Mine.—Large numbers of mines occur together in the stems of the host plants, and it is impossible to trace the individual mines. The greatest number generally occur in the first and second internodes of the plant, and the majority of pupation takes place here also, usually in the region of the node, where the tissues are thicker.

Period of occurrence.—There is one generation a year, the adults emerging in May and June as a rule, although two emerged in late March from pupae reared in the laboratory. Pupation seems to occur in August, and it is in this stage that the winter is spent.

Parasites.—Parasites reared from pupae were *Syntomopus* sp. and *Sphegigaster* sp. (Pteromalidae). Soraur (1953) records *Dacnusa rufipes* Nees (non-British), *D. senilis* (Nees) (Braconidae), *Caudonia agylla* Walk. (Cleonymidae), *Diglyphosema conjugens* Kieff. (Cynipidae), *Phygadeuon rusticella* Bridgm. (Ichneumonidae), *Sphegigaster aculeatus* (Walk.), and *Syntomopus thoracicus* Walk. (Pteromalidae).

Melanagromyza lappae (Loew.)[2]

Host plants.—Recorded from the stems of:

COMPOSITAE.—*Arctium lappa* L., *A. minus* Bernh., *Cirsium arvense* L.
UMBELLIFERAE.—*Angelica sylvestris* L., *Heracleum sphondylium* L.

Mine.—Very similar to that of *M. aeneiventris*.

Period of occurrence.—As in *M. aeneiventris*, there is a single generation per year, and the overwintering stage is the pupa. Pupation occurs in August; adults, according to Hendel (1931–36), occur in May to July. Those reared by me emerged from March to June, but empty pupae were not found in the field until May.

Parasites.—Probable parasites of the larvae which were found in the infested stems were *Habrocytus simulans* Th. (Pteromalidae), and *Bracon* sp. From pupae, *Syntomopus* sp. (Pteromalidae) emerged.

Ophiomyia maura Meigen

Host plants.—Recorded from:

COMPOSITAE.—Leaf mines in *Solidago virgaurea* L. and other species—*Aster* and *Eupatorium*.

UMBELLIFERAE.—Stem mine in *Daucus carota* L. Found by me on *Heracleum sphondylium* L.

Mine.—Mines were not found, but *O. maura* is described as a leaf miner which pupates beneath the epidermis of the leaf. The pupae were found in winter, in the withered tissues at nodes of the stem, where the petioles of leaves had not entirely broken off. The anterior spiracles of the pupa penetrate this tissue, and are just visible from the outside.

No mines were found during the summer, and it seems reasonable to suppose them to be inconspicuous, perhaps confined to the midrib and petiole region of the leaf. The pupation site at the base of the latter seems in accordance with this type of mine.

Period of occurrence.—Hendel postulates two generations, with the adults emerging in June and August. All my pupae were collected between August and March, and the adults emerged from February to May, so that these would all have belonged to the second generation.

Parasites.—Altogether 34 pupae were taken, of which 23 emerged. Eleven of these were parasitized—6 *Dacnusa bathyzona* Mshll. and 5 *Pleurotropis* sp. This is a parasitism rate of nearly 50 per cent. Of those which did not emerge the same was true—4 were parasitized (3 *D. bathyzona*, 1 *Pleurotropis*), 4 were not, the remaining 3 being indeterminable.

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[2] Subsequent to the submission of this paper for publication I have been informed by Mr. K. A. Spencer that, after a study of the genus *Melanagromyza*, he has concluded that the *M. lappae* (Loew) recorded above may in fact be *M. angelicae* (Frost, 1934), and that my *M. aeneiventris* (Fallén) may represent more than one species.

Phytomyza anthrisci Hendel

Host plants.—Recorded from the Umbellifers *Anthriscus cerefolium* (L.) Hoffm., *A. sylvestris* (L.) Bernh., *A. neglecta* Boiss. and Rent., *Chaerophyllum temulum* L., *Daucus carota* L., *Oenanthe phellandrium* Lam. and possibly also from *Myrrhis*. I found it only on *A. sylvestris* and *D. carota* and studied only from the former material.

Mine.—A linear mine, mainly on the upper surface, but with small initial mine on the lower surface. The initial mine has been previously mentioned by Hering (1937) as occurring in *D. carota*. However, as it was always found in *A. sylvestris* also, it would appear to be a regular feature. It constitutes one-third of the mine excavated by the first larval instar.

Hendel describes emergence for pupation as being from a slit on the upper surface of the leaf, but, of the mines examined, only 12 per cent. emerged in this way; 47 per cent. emerged downward, and 41 per cent. by a slit along the edge of the leaf.

Period of occurrence.—Previous work does not make the life cycle very clear. Generally the mines are said to be found from May to July and August, but Hering (1937) states that they can be found also in the winter months, and (1927) that distinct generation peaks do not seem to occur.

In preliminary investigations in 1952 separate generations were certainly not clearly defined. In 1953 the species was studied in greater detail. Ten plots, each 1 metre square, were laid out in an area of dense *Anthriscus sylvestris*. They were examined every week throughout the season, and empty or parasitized mines removed and investigated. This gave the numbers pupating during the previous week, and some idea was gained of the causes and extent of larval mortality. The data obtained are illustrated in fig. 4.

First emergence of adult flies in the laboratory occurred on 24th February, but, although one mine was found on 20th February, 1952, mines, and female flies laying eggs, were not found in the field in 1953 until 4th May. From this date, the number of mines steadily increased, reaching a peak at the end of May, and gradually falling off again until the middle of July, when most of the plants were withered. A few were found again at the end of August and beginning of September. Careful search the previous year had revealed a few mines even in October and November. *Anthriscus sylvestris* plants which had been cut down in the spring usually had a number of leaves at a time when plants left to grow naturally had withered, and a few mines could be found on such leaves during August, when the other plants had died down.

Lengths of stadia.—Hatching seemed to take place mostly on the fifth or sixth day after oviposition. Generally the mouth parts of the developing larva were visible by the fifth day, hatching took place on the sixth, and by the seventh day the larva had completed the initial mine and had already entered the palisade parenchyma. Each larval stadium was two and a half to three days, as in most of the other *Phytomyza* species studied, so that the period from oviposition to pupation was in the region of 14–15 days.

The length of the pupal stadium showed a great deal of variation, but there appeared to be two distinct types of pupae. The first type emerged after 10–24 days, generally 22–23, and the second type emerged after 100 days, ranging from 102–202, but mainly at about 140 days. Both types seemed to occur at all times of the year, but 64 per cent. of all pupae from which adult flies emerged were long term type. It is possible that this figure is rather low, since with these pupae the risk of death by dessication during storage in the laboratory was naturally greater.

It was less easy to estimate the length of adult life, since the flies were under unnatural conditions. None of the reared female flies would oviposit. Copulation was observed, however, between a 10-day-old male and an 8-day-old female. The male died two days later, and the female shortly after, without having laid eggs. One female already laying eggs in the field, continued to do so for 8 days after capture, laying a total of 66 eggs before she died. This would appear to indicate a possible life of at least 20 days or more for the female fly, and 12 days or more for the male.

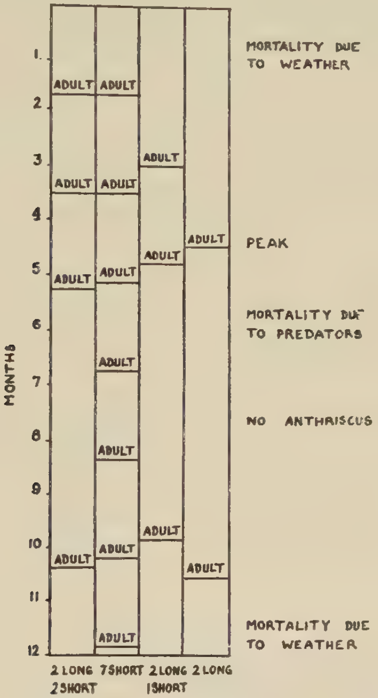

FIG. 3.—Possible variations in the number of generations of *P. anthrisci*.

The discovery of long and short term pupae sheds a certain amount of light on the type of life cycle. The presence or absence of diapause is apparently not influenced by external conditions, since both types of pupae occur together, but the two types serve to explain the lack of definite boundaries to the generations, and the uncertainty which is found in the descriptions of the life cycle.

Generations can thus be either short or long, depending on the type of pupae. If we assume eggs to be laid about 15 or 20 days after emergence of the adult female, in one year two long or seven short generations could occur, or many different combinations of the two types. Since 64 per cent. of collected pupae were of the long term type, there may be a slightly greater tendency for long generations and, if so, the general rule is more likely to be either two long and two short in the year, or two long and one short generation. It must be remembered that, even within the long generations, pupation time is varying from 102–202 days. If these generations were arranged as in fig. 3, the peak which occurs in May is accounted for, but it must be remembered that this is purely diagrammatic—eggs are laid on successive days, so that each generation is not so sharply defined as is shown. In cases other than those illustrated, when the fly emerges at other times of the year, it may encounter adverse conditions. In late July and August it will be difficult to find *Anthriscus sylvestris* leaves, and there will probably be a high mortality from predators. In the winter months, although the leaves will be fairly abundant, weather conditions will not favour long survival of the adult.

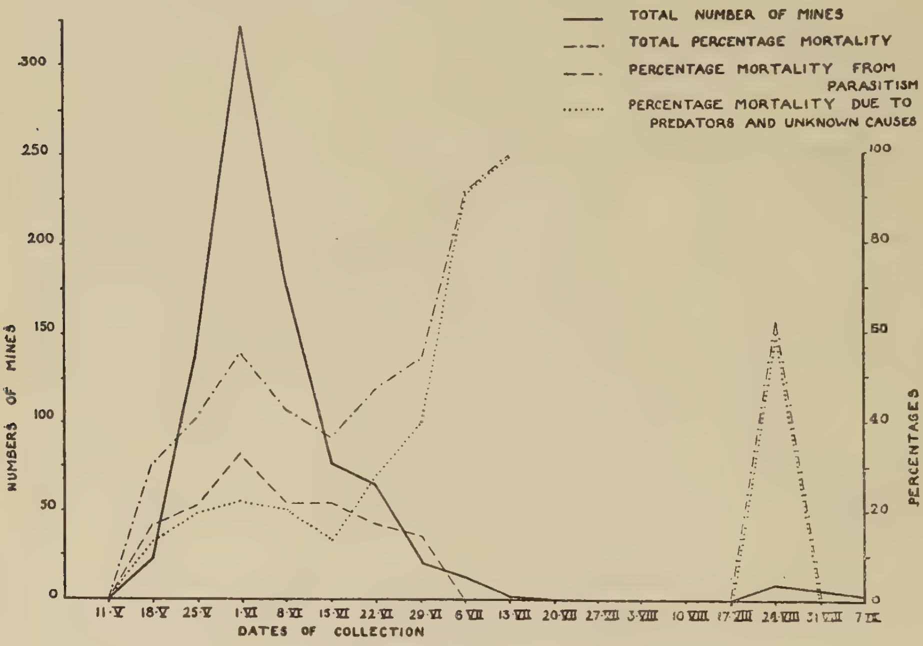

Fig. 4.—The biology of *P. anthrisci*.

Mortality.—I find no reference to parasites, but my investigations indicate the presence of at least five larval and four pupal parasites. Eggs of the latter must be laid in the host larva, but the adult parasite emerges from the pupa. In addition the weekly observations showed a considerable larval mortality not apparently due to parasites. In some mines the section of the leaf containing the larva had been bitten or torn away. In others, merely the top surface of the leaf and the underlying larva had been removed. Sometimes the empty, dry skin of the larva was found, still in the apparently intact mine, and sometimes a dead larva which was not dry.

Birds may have accounted for some of the mortality—e.g. those larvae which had been roughly torn out. Insect predators were probably responsible for much of the rest—Chrysopid larvae, and Anthocorids. Those cases in which the larva was dead but not sucked dry are rather more difficult to account for. It is possible that they may have been attacked by fungi. Hering (1951) suggests that " parasitic fungi must be considered as responsible for the destruction of mining insects on a far wider scale than has been so far realised ".

Fig. 4 shows how the great increase in the number of mines is accompanied by an increase in the number of parasites. The mortality attributable to parasites falls off at the same time as the number of mines decreases, whereas the percentage mortality due to predators and unknown causes continues to rise. In the later mines of August and September mortality from predators and unknown causes is still found, whereas parasitism is absent. This may be correlated with the dependence of parasites on the host and their consequent occurrence at its peak period, while the predators are independent of the variation of a single species, having many different hosts.

It was difficult to rear the larval parasites. The host larva had to be removed from the mine in order to determine the nature of the parasite. Subsequent storage on damp filter paper usually led to mould formation, and the results were difficult to obtain. Until further experiments are carried out to determine the nature of the young stages of each parasite, it is impossible to give detail as to their relative abundance.

The parasites reared from larvae were *Colastes braconius* Hal. (Braconidae), and the Eulophids *Cirrospilus vittatus* Walk., *Solenotus* sp. (? *viridis* Först.), *Chrysocharis* sp. and *Derostenus* sp. *C. braconius* has a pale green larva and was not found often. *Chrysocharis* appeared the commonest type of larval parasite ; it leaves the host larva for pupation a little distance from the host, but still within the mine.

The parasites reared from pupae were *Rhizarcha laevipectus* Thorn. (Braconidae), a Pteromalid, and the Eulophids *Chrysocharis* sp., and *Derostenus* sp.—not the same species as the larval parasites.

Of all the pupae which emerged in 1952 and 1953, 49 per cent. were parasitized—12 per cent. *R. laevipectus*, 6 per cent. Pteromalid sp., 31 per cent. Eulophids.

Phytomyza angelicae Kaltenbach

Hosts.—Recorded from the Umbellifers *Angelica sylvestris* L., and *A. archangelica* L.

Mine.—Blotch mine, described by Hering as being on the upper side of the leaf, i.e. in the palisade parenchyma. Closer examination reveals that the initial mine, which is also of the blotch type, is less close to the upper surface and is thus probably mainly in the spongy parenchyma. It is likely that most of the first larval stadium is spent in this initial mine.

The shape of the mine varies considerably, depending not only on the shape of the leaf, but also on the number of larvae present. It is common to find three or more larvae in one mine.

Hendel states emergence to be by a slit in the underside of the leaf, and this is generally so ; of 50 empty mines examined at one time, only one escaped for pupation by a slit on the upper surface.

Period of occurrence.—Hendel states larvae to be present June–October in 2–3 generations per year. Séguy gives May–August, and Hering (1927) May–June and July–August.

In 1952 the first mine was found on 3rd June, and in 1953 on 10th July.

Table II illustrates the times of year and condition of the material found. It must be remembered that the empty mines from a generation may still be found for a considerable time afterwards.

TABLE II.—*Period of Occurrence of* P. angelicae *Kalt.*

	Month.							
	VI.		VII.		VIII.		IX.	
Larva	x	.	x	X	.	x	.	.
Empty mine	.	.	xX	xX	x	x	.	.
Pupa	.	.	.	R	.	r	.	.
Adult	.	r	.	.	R	R	.	R

x = Found in 1952 ; X = found in 1953 ;
r = reared in 1952 ; R = reared in 1953.

Results for 1952 may indicate a first generation of larvae in June and early July, giving a second generation in August, which emerges in September. Possibly these adults hibernate, but it seems more probable that there should be another generation of larvae from which comes an overwintering pupal stage, since this occurs in many other species. Numbers in 1953 were much reduced, and may indicate the omission of one generation, possibly because of bad weather.

Lengths of stadia.—So far as can be calculated from marked mines, the second larval stadium is about three or four days, and the third four or five, but since the mines are blotch mines and the larvae move about freely in previously excavated parts, the exuviae do not necessarily lie at the furthest point of excavation at the time of ecdysis. The position of the exuvium thus indicates the minimum number of days after hatching (or the maximum before pupation) at which ecdysis took place, but not necessarily the exact number.

Length of the pupal stadium varied somewhat. Pupae collected in June, 1952, emerged in 26–28 days; in August 1952, in 36–38 days; in July, 1953, in 17–25 days.

Mortality.—In 1953, 118 mines were analysed, and from 57 of these, or 48 per cent., the larvae emerged from the mines and pupated; 49, or 42 per cent., contained flat, dry larvae, and from 12, or 10 per cent., the larvae had been torn out. This gives a mortality of just over 50 per cent., probably due to predators.

Pupal parasites were also found—*Chrysocharis* sp. (Eulophidae), and *Opius pallipes* Wesm. (Braconidae). No pupal parasites were taken in 1953.

Séguy records *Dacnusa arsolaris* Nees.

Phytomyza angelicastri Hering.

Host plants.—Recorded only from *Angelica sylvestris* L.

Mine.—Linear mine on the upper surface in the second and third stadia, but with the entire first stadium in an initial mine on the under surface only. Escape for pupation is generally from the upper surface, but not invariably.

Period of occurrence.—Hendel records larvae occuring in August, adults in September. Table III indicates the time when material was obtained. It seems probable that there may be two generations, in June and in late July. As in *P. angelicae*, there arises the problem of a possible third generation from which

Table III.—*Period of Occurrence of* P. angelicastri *Hering.*

	Month.					
	VI.		VII.		VIII.	
Larva	x	X	.	xX	.	.
Mine	.	.	x	xX	x	x
Empty pupa	.	.	R	R	rR	.
Adult	.	.	.	R	.	rR

x=Found in 1952; X=found in 1953; r=reared in 1952; R=reared in 1953.

will come the overwintering pupal stage. It seems likely that there should be such a stage, rather than that the adults survive from August until the following May or June.

Parasites.—*Chrysocharis* sp. (Eulophidae) and *Dacnusa turissa* Nix. were obtained from the pupae.

Phytomyza conopodii Hering.

Host plant.—Leaves of *Conopodium majus* (Gouan) Lor. and Barr.

Mine.—Linear mine, mainly on the upper surface, but with a small initial mine on the lower surface. Emergence from the mine for pupation was either upward, or from the side.

Period of occurrence.—The brief life of the *Conopodium* plants restricts the period when mines may be found. The peak seems to be at the end of May or beginning of June, after which *Conopodium* is withering.

Lengths of stadia.—Only four adults were obtained. Their pupation periods were 17, 18, 130, and 190 days respectively. This suggests, as in *P. anthrisci*, the presence of two types of pupae.

Phytomyza melana Hendel.

Host plant.—Leaves of *Pimpinella saxifraga* L.

Mine.—Linear mine, similar to that of *P. anthrisci*, but without an initial mine on the underside. Callus tissue sometimes present. Emergence was always found to be upward.

Period of occurrence.—Mines were found in July and early August.

Lengths of stadia.—Only three adults were obtained, all having a pupal stadium of 18 days.

Mortality.—There appeared to be a considerable larval mortality due to predators—40–50 per cent. in the counts which were made.

Parasites of larvae were *Hemiptarsenus anementus* Walk. and *Solenotus* sp. (? *viridis* Först.) (Eulophidae). *Solenotus* also emerged from pupae, and *Derostenus* sp. was another pupal parasite.

Phytomyza obscurella Fallén.

Host plants.—Leaves of *Aegopodium podagraria* L.

Mine.—Linear mine, entirely upper surface. Emergence for pupation is not always upward, as given by Hendel; the ratio of upper to lower surface emergence was found to be 2 : 1.

Period of occurrence.—Hering gives this as March, April, September, and October. Séguy says that there are several generations a year from March to November, and Hendel gives March to October.

Mines did not occur in the area studied until May, but between May and October some could be found at all times, although the successive generations were not well defined.

Lengths of stadia.—Length of time between oviposition and hatching was about six or seven days. The first larval stadium was about three days, the second two to four days, and the third three to four and a half days. The length of the pupal stadium varied considerably. Large numbers of pupae were collected in November, 1952, and, although the pupae were all treated identically, dates of emergence varied extensively. Of the pupae reared, flies were obtained from 153 : 30 of these emerged after 24–45 days, usually about 30 days. The remainder emerged after more than 172 days, one after as many as 307 days' pupation, but the majority between 220 and 300 days. All long-term pupae were obtained in November, and four short term. Pupae from May, June and August were short term. It, therefore, seems likely that the majority of short-term pupae occur in spring and summer, but that later pupae are long term. Refrigeration experiments with pupae seemed to indicate that the diapause was, at this stage, unaffected by temperature.

Fecundity.—Since none of the adults reared from pupae laid eggs, the possible number which can be laid is not known, but the greatest number laid by a female captured in the field was 61, laid within four days.

Mortality.—Larvae from 117 mines were examined in June, 1953, and it was found that mortality attributable to predators and unknown causes was 11 per cent. in the first instar, 51 per cent. in the second instar, and 38 per cent. in the third. This is possibly because in the first instar the mine is still very small and is less conspicuous than that of the second and third instar. At the same time, parasitism in the three instars was 0 per cent., 9 per cent., and 11 per cent. respectively.

Larval parasites successfully reared were *Colastes braconius* Hal. (Braconidae), and *Cirrospilus vittatus* Walk. (Eulophidae). Pupal parasites were *Dacnusa turissa* Nix. (Braconidae) and *Derostenus* sp. (Eulophidae). The latter were the commoner. Of 128 emergences from the pupae collected in November only one was a parasite—*Derostenus*—so it would appear that there is a much lower parasitism rate in this month than in June and July, when the percentage parasitism of pupae was 30–35 per cent. Larval parasitism in November also seemed less.

Phytomyza silae Hering.

Host plant.—*Silaum silaus* (L) Schinz. and Thell.

Mine.—Linear mine, with the entire first stadium in an initial mine on the leaf underside. Emergence for pupation was upward in all the specimens found.

Period of occurrence.—Mines in July and August. Not found earlier than July, because the *Silaum* had not then grown.

Lengths of stadia.—Second stadia measured were two and a half days, and third three to four days. Pupae in late August emerged after 27 and 28 days.

Mortality.—Mortality due to predators did not seem very high. Parasites emerged from the pupae collected, and were found to be *Priapsis dice* Nix.

(Braconidae). Only three specimens of this species have been found before, none from this country, and this appears to be the first host record. Eight specimens were obtained. *Chrysocharis* sp. also emerged from pupae.

Phytomyza sphondylii Robineau-Desvoidy.

Host plants.—Recorded from leaves of *Heracleum sphondylium* L., *H. persicum* Desf., *Pastinaca sativa* L., *Aegopodium podagraria* L., but I did not find it on the latter.

Mine.—Linear mine, entirely on the upper surface of the leaf, often following the veins. Emergence for pupation always downwards. Callus tissue sometimes present.

Period of occurrence.—Séguy gives this as May–October ; Hering as larvae in May–June, adult in July, and larvae in July–August ; Hendel also gives two generations of larvae, in May–June and August–September.

Not enough data were collected either to confirm or refute the two-generation theory. In 1952 the species was not studied in detail, although mines were obtained from mid-June to August. In 1953, there was very much less material, but this was found between the same dates as the previous year. Pupae obtained in June and July emerged in July and August and may have given rise to a second generation.

Mortality.—In 1952 there was heavy larval mortality and not a single adult fly was obtained from collection in this year. In one area 55 mines were examined in July, of which only one contained a living larva. The remainder comprised 10 parasitised larvae and 44 in which the cause of death was uncertain, but probably due to predators. Whether because of this high mortality or for some other reason, 1953 saw a great drop in the abundance of the species in all areas. It was thus less easy to find the mines, but of those obtained the larval mortality was lower. On the same date as the previous year 61 mines from the same area were examined : 20 of the larva were living or had already emerged from the mine for pupation, 8 were parasitised, 33 were destroyed by predators. This gives a percentage ratio of 33 : 13 : 54, compared with 2 : 18 : 80 in the previous year.

The only larval parasite reared was *Colastes braconius* Hal. From pupae, *Dacnusa bellina* Nix. (Braconidae), *Lamprotatus* sp. (Lamprotatidae), and *Chrysocharis* sp. (Eulophidae) were found.

Phytomyza tordylii Hering.

Host plant.—Leaves of *Torilis japonica* (Houtt.) DC.

Mine.—Very similar in all respects to that of *P. anthrisci*. The surface of emergence varies considerably. Of 60 empty mines analysed 16 (27 per cent.) emerged upward, 22 (37 per cent.) downward, and the same number by a lateral slit.

Period of occurrence.—This is given by Séguy as June–September. Mines were found here in July.

Lengths of stadia.—Of the pupae taken, only four emerged, after 16, 17, 20, and 57 days respectively.

Mortality.—There was considerable larval mortality due to predators. *Chrysocharis* sp. emerged from pupae.

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SUMMARY.

Studies of the biology and parasitism of thirteen species of Agromyzidae occurring on Umbellifers in Berkshire are described.

It was possible to study some species in greater detail than others, but among the *Phytomyza* species a number of features may be common to all. The lengths of larval stadia seemed to be in the region of two to four days, and in *P. anthrisci* and *P. obscurella* the egg stadium appeared to be about six days.

The pupal stadium was found to show considerable variation, and the presence of two types of pupae, long and short term, is suggested for at least some of the species. Whatever the factor which induces diapause in the long-term pupae, it must be innate in some species, since both types were collected and reared together. Species with a shorter season than *P. anthrisci* and *P. obscurella* are assumed to overwinter as pupae, and in these temperature may play a part in the induction or length of diapause, but it is not yet possible to be definite.

The absolute fecundity could not be found, since the laboratory reared females would not breed, but it may be significant that in both *P. anthrisci* and *P. obscurella* the maximum for captured specimens was similar—61 and 66.

Although parasitism is generally rather high, little previous work seems to have been done on the parasites, as is indicated by the few previous records quoted. Consequently, a number of new host records have been made here, the most notable being *Priapsis dice* Nix., from *P. silae.*

Not all the parasites found are host specific. *Colastes braconius* Hal. was found to occur on *P. anthrisci*, *sphondylii*, and *obscurella*. *Dacnusa turissa* Nix. occurs from *P. angelicastri* and *obscurella*. *Cirrospilus vittatus* Walk. and *Derostenus* sp. were taken from *P. anthrisci* and *obscurella*; *Solenotus* sp. (? *viridis* Först.) and a different *Derostenus* sp. from *P. anthrisci* and *melana*. A number of *Chrysocharis* spp. occurred on many *Phytomyza* species, but have not been separated.

It is evident that further study is desirable, and would yield much interesting material.

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THE LARVA OF AN EAST AFRICAN CADDIS FLY, *CHEUMATOPSYCHE COPIOSA* KIMMINS (HYDROPSYCHIDAE).

By N. E. Hickin, Ph.D., F.R.E.S.

Larvae of this species are very common in the same situations at the Ripon Falls, Uganda, where *Phanostoma senegalense* Brauer occurs in such large numbers. The dead bodies of the adults were present in such numbers with those of *P. senegalense* as, no doubt, to make a contribution to the stench. A number of larvae collected on 3rd May, 1954 were maintained in an aquarium at Jinja, and adults emerged on 28th May to 4th June, 1954. These were identified by Mr. D. E. Kimmins.

The drowning of the Ripon Falls by the construction of the Owen Falls Dam is bound to have a depressing effect on the population of this insect, as it occurred on the Lake Victoria side of the Falls at the point where the water had considerable movement prior to entering the actual fall of water.

The larvae construct loose shelters of a silk-like material quite unlike the tough tube made by *P. senegalense* and quickly made such shelters when placed in the aquarium.

Larva : Campodeiform ; length 9·0 mm., width 1·1 mm. Almost the whole body covered with short dark curved hairs. Head yellowish with clypeus dark brown. Pronotum and genae yellowish-brown. Meso- and metanota yellowish, lateral margins black. Abdomen bright apple green to bluish-green. Last abdominal segment whitish. All thoracic nota sclerotised. *Head :* Ovate, clypeus broad with pattern of small white spots, as shown in figure, oval margin of clypeus with median shallow excision and lateral deeper excisions. Antennae small. On the ventral surface the genae are slightly darker along the genal suture.

Summary.

The larva of *Cheumatopsyche copiosa* Kimmins is described and figured.

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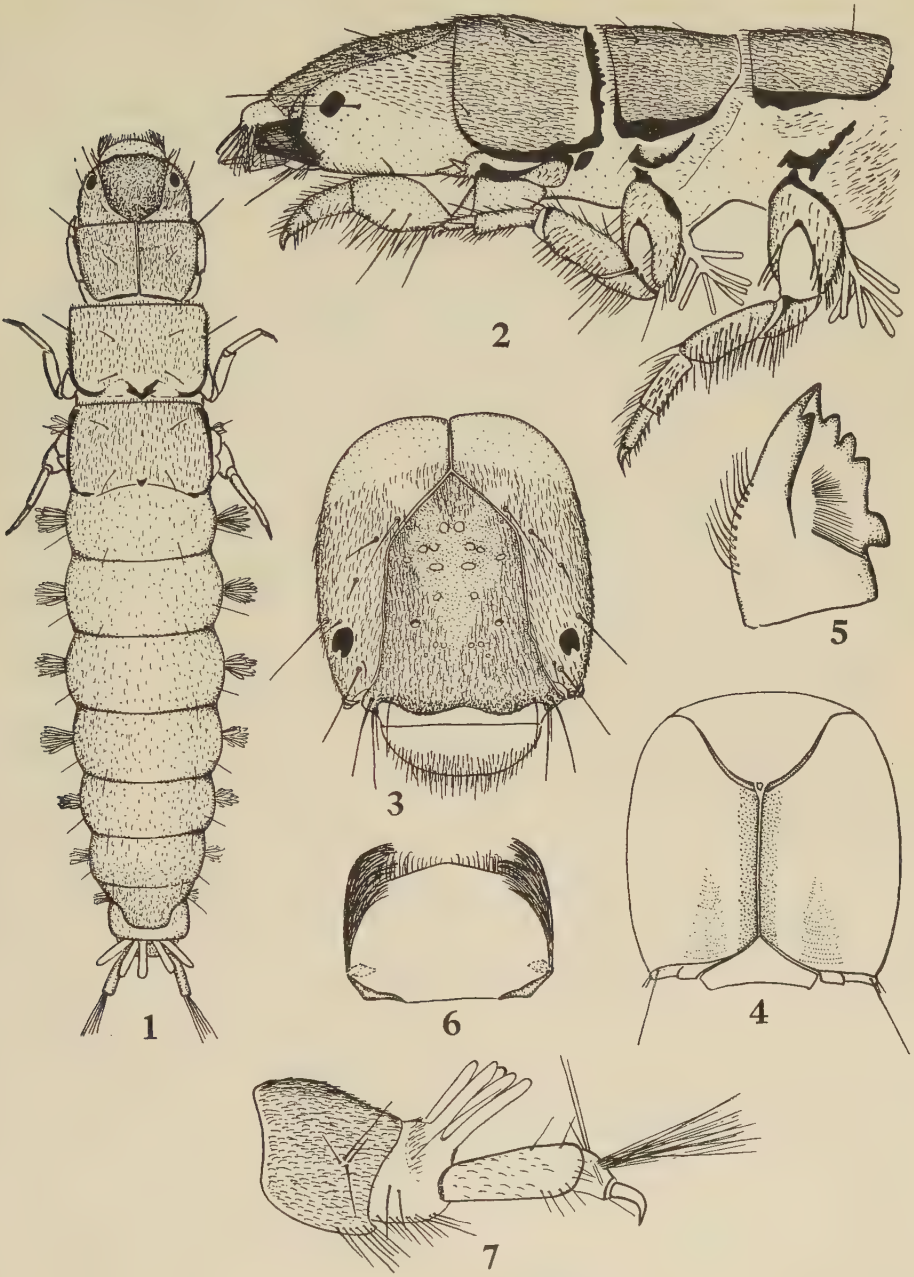

Figs. 1–7.—Larva of *Cheumatopsyche copiosa* Kimmins. (1) Larva from above. (2) Head, thorax and legs from the side. (3) Head from the front. (4) Head from below. (5) Left mandible from above. (6) Labrum from below. (7) Anal segment.

AN INVESTIGATION INTO THE POSSIBLE EFFECTS OF MOONLIGHT ON THE ACTIVITY OF INSECTS IN THE FIELD.

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It has been known for many years that the lunar cycle is associated with changes in the activity of certain animals, but most of the established cases are in marine animals, and the effect may be partly at least through the tides.

In the case of insects it has long been a belief among amateur entomologists that it is little use collecting moths on a night when the moon is near full, as very few will be flying round. It must, however, be remembered that the average person does not notice the phase of the moon unless the sky is clear, and in general clear nights mean cold nights, so that the effect of temperature and moonlight on a clear night might easily be confused.

Hora (1927) brought forward some evidence that May-flies (Ephemeridae) tend to emerge and swarm in great numbers at or near full moon. More recently some confirmation of this has been produced by Hartland-Rowe (1955) in East Africa.

When nocturnal insects are captured in light traps there is a very definite periodicity in the numbers, with low catches at or near full moon and high catches in the new moon period. This has been found both in the tropics, as for example by Pagden (1932) with two Pyralid moths in Malaya, and in Britain (Williams, 1936 and 1940). In these latter observations the geometric mean catch in the new moon week was two to four times that in the full moon week. Hosni, in an unpublished thesis (1953), showed that the same result occurred when an ultra-violet light was used.

It was, however, considered that these differences were unlikely to be due to a direct effect of the light on the insect, and were more likely to be due to a reduction of the efficiency of the trap at full moon ; in other words the effect was probably an artifact. The brightness of the light in the trap, relative to the illumination of the surrounding area, would be less on moonlight nights than on nights with no moon.

From July to November 1950, B. P. Singh collected insects every night by means of a suction trap, in which the efficiency is in no way dependent on relative illumination. Five lunar cycles were covered and the results, which will be discussed more fully later, gave some evidence of a regular cycle with nearly four times as many insects, on an average, in the new moon week as in the full moon week (Williams and Singh, 1951).

If this result were real it would imply an effect of moonlight on the insects which might occur in one or more of the following ways :

(1) An effect on the actual numbers of the population, which seemed unlikely.

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(2) A direct effect on their activity; resulting in fewer insects being active at times of bright moonlight.

(3) An effect on their flying habits.

In this last alternative one possibility, suggested by some not very convincing evidence in mosquitos, was that the insects might fly more in shaded places and less in the open. A second possibility was that they might fly higher in the air at full moon, thus reducing the density of population at lower levels. It would follow from this that at some unknown higher level the population density, and hence the captures in a trap, should be greater at full moon than at new moon.

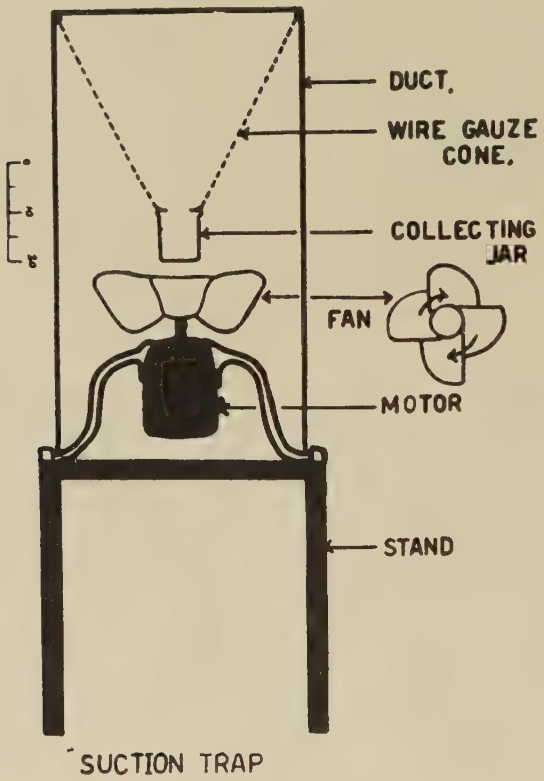

Fig. 1.—Diagrammatic section of the suction trap. (Scale in cms.).

To obtain more information on the reality of this lunar cycle, and to try to trace the nature of the effect, if any, the following experiments were carried out at Rothamsted in the years 1950 to 1953. Trapping was done with suction traps 18 inches in diameter, with the fan below the net in a metal cylinder; thus the air was drawn through the net (fig. 1). The insects were collected into a small bottle of alcohol at the tip of the net. Each trap filtered the insects from approximately 116,000 cubic feet of air per hour. They were working from half an hour after sunset to half an hour before sunrise.

Experiment I.—Singh's work in 1950. A single trap in the garden of

Rothamsted Lodge, on a lawn with various trees, bushes and flower beds. The trap was at a height of five feet.

Experiment II.—From May to November 1951 Singh ran two traps in the grounds of Rothamsted Manor, about half a mile from the 1950 site. One trap (X) was on an open lawn just on the edge of a mixed woodland of about eight acres. The other trap (Y) was inside the woodland. Both were at five feet.

Experiment III.—In 1952 and 1953, S. el Ziady ran two traps in the garden of Rothamsted Lodge (same site as Expt. I), one at a height of 5 feet and the other on a tower 30 feet above the ground. The traps were working from April to October but, owing to some breakdowns and unavoidable delays in getting replacement motors, there were only six months in which both traps were working simultaneously.

In all the analyses the number of insects captured each night was expressed as log $(n + 1)$, and all means were calculated on the log scale. In the 1952 and 1953 results only Diptera were included. In the 1950 and 1951 results all insects were included, but, as the Diptera nearly always made up 90 to 100 per cent. of the catch, there is practically no difference. A recalculation of some of Singh's results using Diptera only made very small differences in the second decimal place of the average, and practically no measurable difference in the comparisons.

The catches in 1950, 1952 and 1953 were corrected to allow approximately for departures from the normal of minimum temperatures and wind. The 1951 results have not been so corrected.

THE 1950 EXPERIMENTS.

Table I shows the mean log $(n + 1)$ catch for each lunar quarter (three days on either side of the date of full moon, etc.) for five lunar cycles from July to November 1950, and figure 2 shows the same results graphically. The mean values for the five repetitions show a regular gradation from high at new moon to low at full moon, the difference in log being 0·66, equal to change of over four times. It will be seen, however, that there is very considerable variation in pattern in the different lunar months, the peak occurring in the first quarter in both July and August. Much of the difference in the final average is determined by the lunar month in November. Without this month (see Table I and fig. 2) the mean catch in the first quarter is very slightly higher than at new

TABLE I.—*Mean log* (n + 1) *catch in each quarter of the lunar cycle during* 1950. *All insects. Trap at a height of five feet.*

1950.	Full moon.	Last quarter.	New moon.	First quarter.	Mean for month.
July . . .	2·73	2·82	3·12	3·20	2·97
August . .	3·28	3·01	3·26	3·42	3·24
September .	3·13	2·96	3·22	3·12	3·11
October . .	1·96	3·06	3·40	3·32	2·94
November . .	0·97	1·69	2·33	0·84	1·46
All five months .	2·41	2·71	3·07	2·78	2·74
Four months excl. November	2·78	2·94	3·25	3·27	3·06

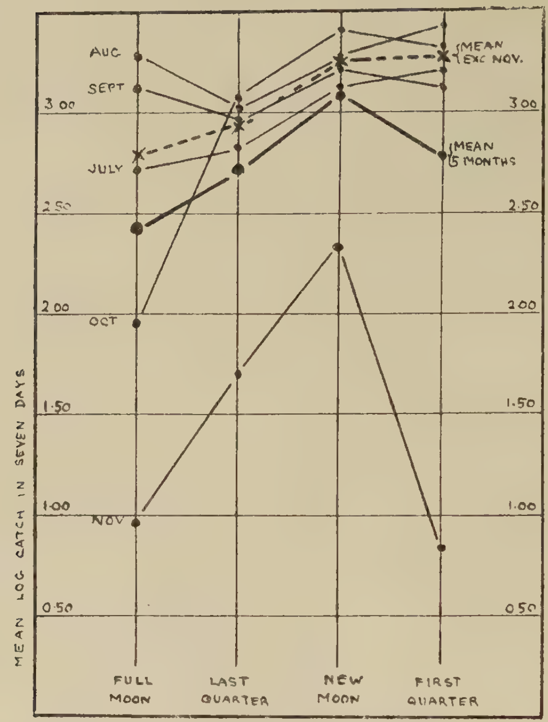

FIG. 2.—Mean log $(n + 1)$ catch in the seven-day periods round each quarter of five lunar months in 1950, with the mean for each quarter, for all five months together, and for the four months excluding November.

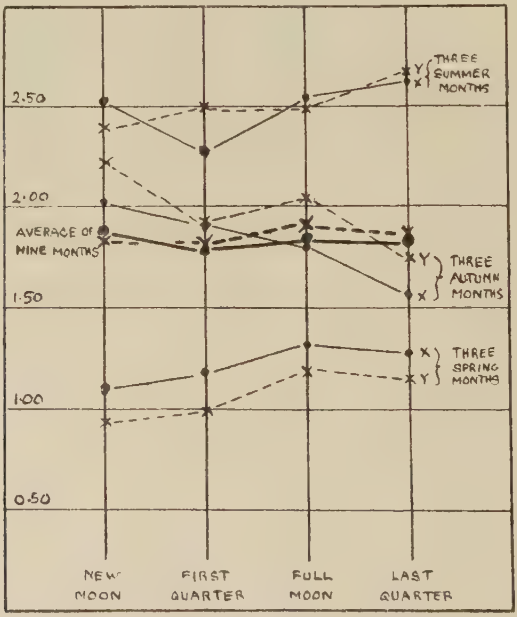

FIG. 3.—Mean log $(n + 1)$ catch in each lunar quarter in spring, summer and autumn in 1951. Trap X (solid line) outside the wood, and trap Y (broken line) inside wood.

moon, but still the catch at full moon is considerably lower, with a log difference of nearly ·50. The results are suggestive of a cycle, which is, however, more obvious in the autumn months of October and November, and indefinite in the earlier months.

THE 1951 EXPERIMENTS.

From March to November 1951 two similar traps were used, one inside a small wood (Y) and one just outside (X), about 80 yards from the first. The outer trap was exposed to direct moonlight, but moonlight could penetrate to trap Y only in early spring and late autumn ; in the summer and early autumn there was a thick overhead canopy.

The mean log $(n + 1)$ catch for each seven day period is shown in Table II and figure 3. There is a slight and expected rise from new moon to last quarter in the spring months, when the population as a whole is rising, and a definite

TABLE II.—1951 *Experiments. Mean log catch of all insects in each quarter of the lunar cycle in two traps: X, outside a wood and Y, within it.*

	New moon.	First quarter.	Full moon.	Last quarter.	Whole cycle.
Trap X :					
March	1·02	1·27	0·67	0·59	0·89
April	1·03	1·30	1·45	1·21	1·25
May	1·26	0·91	1·80	2·03	1·50
Spring	1·10	1·16	1·31	1·28	1·21
June	2·18	2·07	2·43	2·70	2·35
July	2·79	2·35	2·76	2·75	2·66
August	2·57	2·35	2·36	2·41	2·42
Summer	2·51	2·26	2·52	2·62	2·48
September	2·22	2·55	2·18	1·97	2·23
October	1·86	1·46	1·39	1·39	1·53
November	1·94	1·76	17·4	1·30	1·69
Autumn	2·01	1·92	1·77	1·55	1·81
All months	1·87	1·78	1·83	1·82	1·83
Trap Y :					
March	0·31	1·18	0·93	0·61	0·76
April	1·47	0·96	1·19	1·14	1·19
May	0·91	0·81	1·64	1·69	1·26
Spring	0·93	0·98	1·19	1·15	1·06
June	1·73	2·70	2·36	2·61	2·35
July	2·86	2·54	2·70	2·72	2·71
August	2·56	2·24	2·42	2·66	2·47
Summer	2·38	2·49	2·49	2·66	2·51
September	2·56	2·36	2·38	2·25	2·39
October	1·99	1·39	1·58	1·31	1·57
November	2·11	2·04	2·15	1·65	1·99
Autumn	2·22	1·93	2·04	1·74	1·74
All months	1·84	1·80	1·91	1·85	1·85

fall from new moon to last quarter in the autumn, when the population is falling. Otherwise there appears to be no indication of any lunar cycle. In the trap outside the wood the catch is very slightly greater at new moon than at full moon : inside the wood the reverse is the case, but the differences are only ·04 and ·07 respectively (equivalent to about 10 per cent. and 18 per cent. difference), and neither is significant in view of the very great variation from cycle to cycle.

To test the possibility of any regular differences between the two traps—either associated or not with the lunar cycle—Table III shows the difference in log catch (trap X – trap Y) for the nine cycles. The greatest difference is at full moon —0·10 (i.e. more inside the wood than outside), but this is completely accounted for by a difference of —0·27 in the three autumn months. It is interesting to note that the trap outside the wood caught more insects than that inside in the spring, but the reverse was the case in the autumn.

TABLE III.—1951 *Experiments. Difference between the mean log catches in each lunar quarter in traps inside and outside the woodland. The positive sign indicates more insects in the trap outside the wood.*

1951.	New moon.	First quarter.	Full moon.	Last quarter.	Lunar month.
March	+0·71	+0·09	—0·26	—0·02	+0·13
April	—0·44	+0·34	+0·26	+0·07	+0·06
May	+0·35	+0·10	+0·16	+0·34	+0·24
Three Spring months .	+0·17	+0·18	+0·06	+0·13	+0·14
June	+0·45	—0·63	+0·07	+0·09	nil
July	—0·07	—0·19	+0·06	+0·03	—0·05
August . . .	+0·01	+0·11	—0·06	—0·25	—0·05
Three Summer months	+0·13	—0·23	+0·03	—0·04	—0·03
September . . .	—0·34	+0·19	—0·20	—0·28	—0·16
October . . .	—0·13	+0·07	—0·19	+0·08	—0·04
November . . .	—0·17	—0·28	—0·39	—0·35	—0·30
Three Autumn months	—0·21	—0·01	—0·27	—0·19	—0·17
All nine months .	+0·03	—0·02	—0·10	—0·03	—0·03

The evidence does not lend support to the idea of a regular lunar cycle of activity either in the wood or outside.

THE 1952–1953 EXPERIMENTS (S. el Ziady.).

In these two years the two traps were returned to the garden at Rothamsted Lodge, where the more definite evidence of a lunar cycle had been obtained in 1950. One was at 5 feet and the other at 30 feet from the ground, to see if there was any difference in level of flight at different phases of the moon.

The lower trap was working during six months in 1952 and two months in 1953, the upper trap during four months in 1952 and five in 1953. The two were working simultaneously for six months only. The results are shown in Table IV and figure 4.

TABLE IV.—*Mean log catch of Diptera in each lunar quarter in* 1952 and 1953 *for two traps, one at a height of five feet and the other at thirty feet.*

1952.		Full moon.	Last quarter.	New moon.	First quarter.	Lunar month.
April	Low	2·24	2·94	2·80	2·74	2·68
June	Low	3·69	3·51	3·77	3·54	3·63
July	Low	3·57	3·68	3·37	3·13	3·44
	High	2·60	2·71	2·36	2·09	2·44
August	Low	3·02	3·03	2·71	3·28	3·01
	High	1·89	2·17	1·56	2·15	1·94
September	Low	2·26	2·23	2·11	2·52	2·28
	High	1·17	1·53	1·66	1·75	1·66
October	Low	1·88	2·47	2·09	2·83	2·32
	High	1·89	1·24	0·78	1·88	1·45
1953.						
May	Low	2·23	1·53	1·54	1·84	1·79
	High	1·69	1·69	0·83	0·78	1·18
June	High	1·86	1·42	1·69	1·88	1·71
July	High	2·56	2·40	2·71	2·39	2·52
August	High	2·68	2·36	2·64	2·74	2·61
September	Low	2·59	3·08	2·80	2·61	2·77
	High	2·18	2·62	2·40	2·25	2·36
Mean, all months	Low	2·69	2·81	2·65	2·81	2·74
	High	2·12	1·92	1·84	2·06	1·99
Six months, both traps	Low	2·59	2·67	2·44	2·70	2·60
	High	1·99	1·85	1·59	1·92	1·84
Both traps, excl. Oct.	Low	2·73	2·71	2·51	2·68	2·66
	High	2·01	1·97	1·75	1·93	1·92

It will be seen that the lower trap showed no evidence of lunar periodicity, either in the total of eight months or in the six months of simultaneous working. There are small peaks at first and last quarters, and small dips at both new and full moon. In the upper trap there is slight indication of a cycle with the lowest captures at new moon and the highest at full moon; but once again much of this is due to the catches in the single autumn month of October, when the average catch in the new moon week fell to only five insects per night.

There remains the question whether there is any evidence of a cyclic change between the two traps. Table V and figure 5 show the differences between the log $(n + 1)$ for the two traps, the lower trap having a larger average catch in every period except at the full moon in October 1952, when the upper trap exceeded it by a very small margin.

On the average of the six lunar cycles there is the greatest difference at new moon and the least at full moon, but once again this is almost completely accounted for by conditions in one cycle, that in October 1952. Without this month there is practically no change in the log difference, and hence in the ratio of the catches. The average difference of 0·74 indicates that the lower trap is catching approximately five and a half times as many insects as the upper trap.

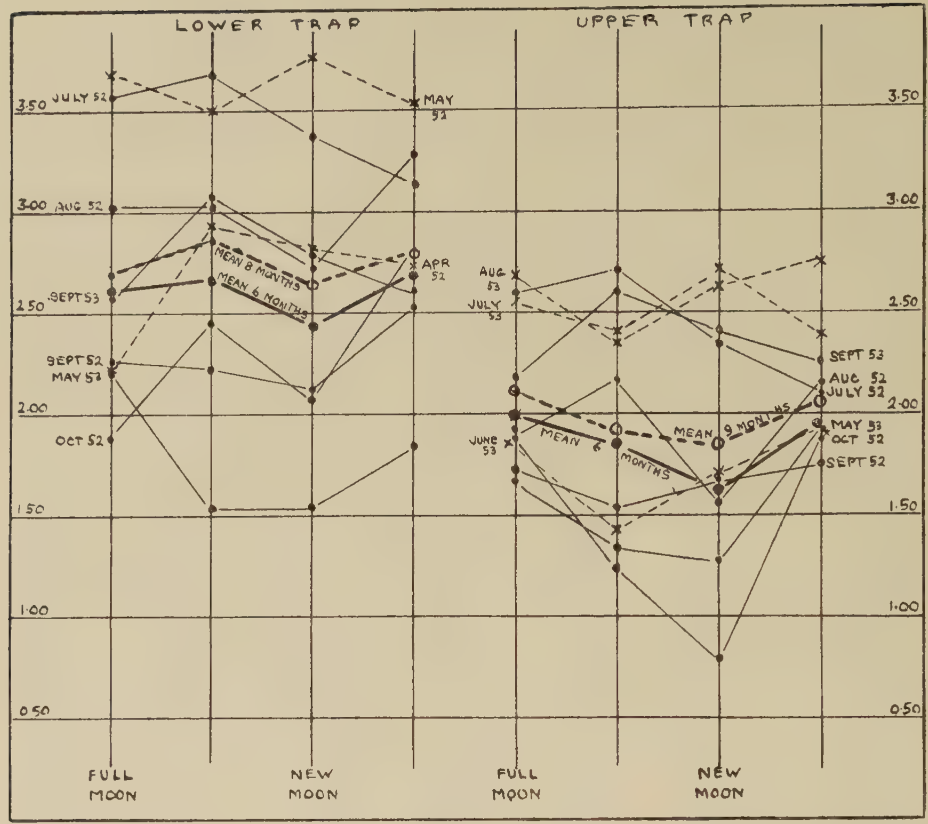

FIG. 4.—Mean log ($n + 1$) catch in two suction traps in 1952 and 1953, one at a height of five feet and the other at thirty feet. Solid lines represent the months when both traps were working; dotted lines when only one or the other was in action.

TABLE V.—*Difference in log catch of Diptera between the upper and lower traps in* 1952 *and* 1953 *in lunar cycle quarters. The lower trap has the higher catch except in the full moon week of October* 1952.

1952.	Full moon.	Last quarter.	New moon.	First quarter.	Lunar month.
July	0·97	0·97	1·01	1·04	1·00
August	1·13	0·86	1·15	1·13	1·07
September	0·55	0·70	0·45	0·77	0·62
October	–0·01	1·23	1·31	0·95	0·87
1953:					
May	0·54	0·70	0·76	0·42	0·61
September	0·41	0·46	0·40	0·36	0·41
Mean—6 months	0·60	0·82	0·85	0·78	0·76
Mean excl. October, 1952	0·72	0·73	0·75	0·74	0·74

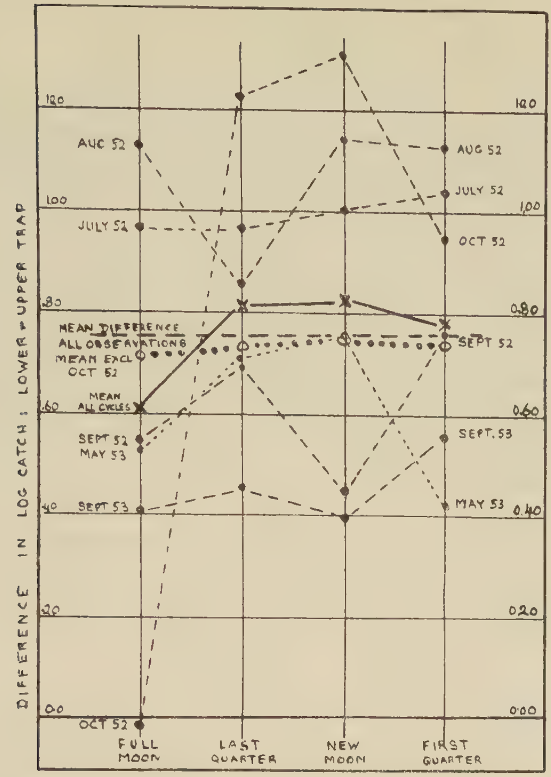

Fig. 5.—Mean log difference in catch between the upper and lower traps in the four quarters of six lunar months in 1952 and 1953. In all cases, except the full moon week in October 1952, the lower trap caught more insects than the upper.

Discussion.

It would appear that none of the trapping carried out with the suction traps in 1951, 1952 or 1953 supported the suggestion, arising from the 1950 results, that there was any regular lunar cycle in the number of insects caught. Most of the small differences found have been due to conditions in one or two lunar cycles, while the majority show no regular differences. It should be noted that the exceptional months are both in late autumn, when, however, catches are low. The effect might, therefore, be due to a greater sensitivity of some autumn Diptera (perhaps the *Trichocera*), or to the large relative error existing when catches are small. The latter is probably the correct interpretation.

Leaving aside the question of a lunar cycle in the total catch per night, the data available show in 1951 no cyclic difference between the catches inside and outside the wood, and in 1952 and 1953 no cyclic difference between the catches in a trap at five feet above the ground and one at thirty feet. It seems probable that the apparent cycle obtained in 1950 was accidental and of no biological significance.

We are, therefore, still without any evidence of an effect of moonlight on the activity or distribution of night-flying insects, except in the case of some aquatic species, where the influence appears to be on the emergence from the water and so on the size of the adult winged population.

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A STUDY OF THE POPULATIONS OF THE RABBIT FLEA *SPILOPSYLLUS CUNICULI* (DALE) ON THE WILD RABBIT *ORYCTOLAGUS CUNICULUS* IN NORTH-EAST SCOTLAND.

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Introduction.

The results of 15 months' field work on the populations of the rabbit flea *Spilopsyllus cuniculi* (Dale), 1878, occurring on the wild rabbit are recorded in this paper. A short preliminary note has already been printed on this subject (Allan and Shanks, 1955) as, up to that time, little was known regarding flea populations present on rabbits. It was intended to continue these observations over a period of several years but, since the introduction of the virus disease myxomatosis in the area, insufficient rabbits have been available to continue this study. In view of the several interesting facts which have been established and the improbability of further observations of this type being made in this country in the near future, it is thought advisable to publish the data already collected.

Little is yet known regarding the biology of the rabbit flea, indeed of fleas in general, and to this extent these results may be regarded as forming a basis for a more complete understanding of flea biology. There is practically no literature dealing with the subject in detail, excepting the few fleas of medical importance. Since *Spilopsyllus cuniculi* has been proved to be a vector of myxomatosis (Lockley, 1954) it is hoped that this paper will be of special interest to those concerned with the virus disease.

Habitat.

The observations were carried out on Ballogie Estate, Aberdeenshire, an area which incorporates farmland, rough pasture and woodland, the latter being partially devastated during the winter gale of 31st January, 1953. Much of the estate is covered with heather and bracken and it was from this type of habitat that most of the rabbits were taken. The area concerned lies at just over 400 ft. above mean sea level.

In spite of the efforts of several keepers to enforce rabbit control the area abounded with rabbits before the advent of myxomatosis.

Methods.

For the purpose of the counts, rabbits were examined at fortnightly intervals. These were removed from the trap and killed immediately prior to examination; rabbits which had died of exposure in the trap were not included in the count.

Only fully grown rabbits were examined, since these may harbour more parasites than immature rabbits. From observation this seems to be the case. From 10 immature rabbits examined independently from the usual flea counts, an average of 14·6 fleas were collected on 30th April, 1954, whereas the average was 150·5 on that same day from 20 adult rabbits. The age of the rabbit did not appear to influence the location of the fleas on the rabbit's body, although this was not closely investigated.

The fleas were removed from the host with a pair of fine forceps in the field, since, during warm weather especially, the fleas present tend to run about the host a few moments after it has been killed. Three tubes filled with 70 per cent. alcohol were used for each rabbit, a tube for each group of fleas from the ears, head and remainder of the body. The fleas were later counted and sexed in the laboratory.

At some periods of the year a number of fleas are to be found on the body of the rabbit where it is more difficult to remove them but, if the hand is held close to the body surface, the fleas quickly rise to the top of the host's hair.

It was found that the rabbits normally lost their parasites within a few hours after death, especially in warm weather, although, on occasion, during low temperatures fleas were found attached to the ears as much as forty-eight hours after the rabbit had been killed. These were still very much alive and quickly dispersed if disturbed.

RESULTS.

Each fortnight commencing 24th December, 1953, twenty rabbits, of which ten were male and ten female, were trapped at the Ballogie site and counts made of the number of male and number of female fleas on each rabbit. This was continued until 4th March, 1955, when myxomatosis prevented further counts being made.

The variance of each set of counts was dependent on the mean for the set and, as these means varied considerably, it was necessary to use a transformation, the one used being

$$Y = \log(\text{count} + 1)$$

An analysis of variance was carried out on the transformed count (Table I) which showed, of course, a highly significant difference between fortnights but also a highly significant difference between numbers on male as compared with female rabbits in the different fortnights.

TABLE I.—*Analysis of variance* (1954 *only*).

	d.f.	S.O.S.	M.S.	V.R.
Fortnights . . .	23	122·203747	5·313206	
Sexes	1	0·003543	0·003543	
Fortnights × sexes . .	23	6·711622	0·291810	1·808*
Residual . . .	432	69·705454	0·161355	
Total . .	479	198·624366		

The mean values of total counts for all rabbits, and male and female rabbits separately, were transformed back to the original units—the values for the male and female rabbits being plotted as a time series (fig. 1). This graph shows a gradual increase in the number of fleas per rabbit between fortnights 2 and 4 (8.i.54 to 5.ii.54), followed by a large increase at fortnight 6 (5.iii.54). It is apparent that this increase in population occurred mainly on the doe rabbit at first, but by fortnight number 10 (30.iv.54) the population was equally divided

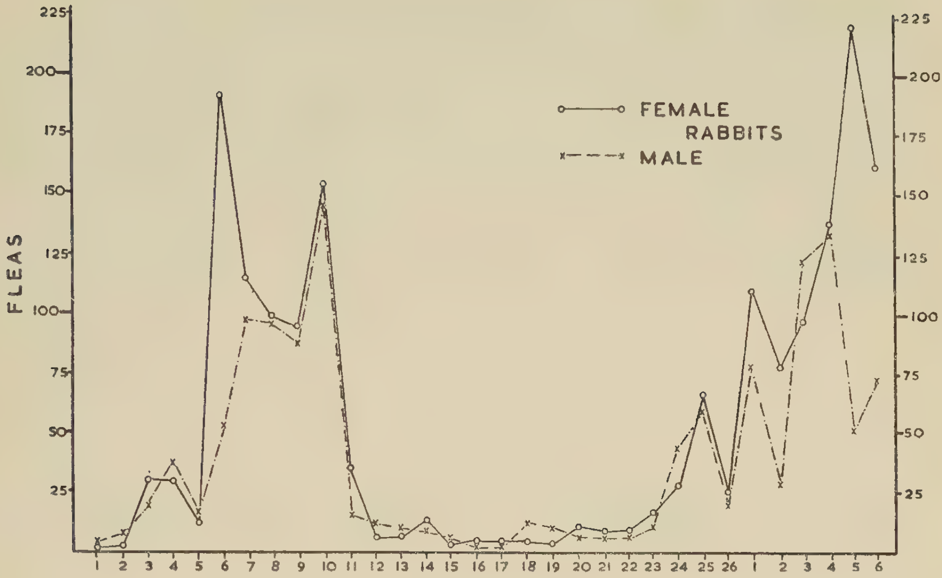

Fig. 1.—Average number of fleas per rabbit.

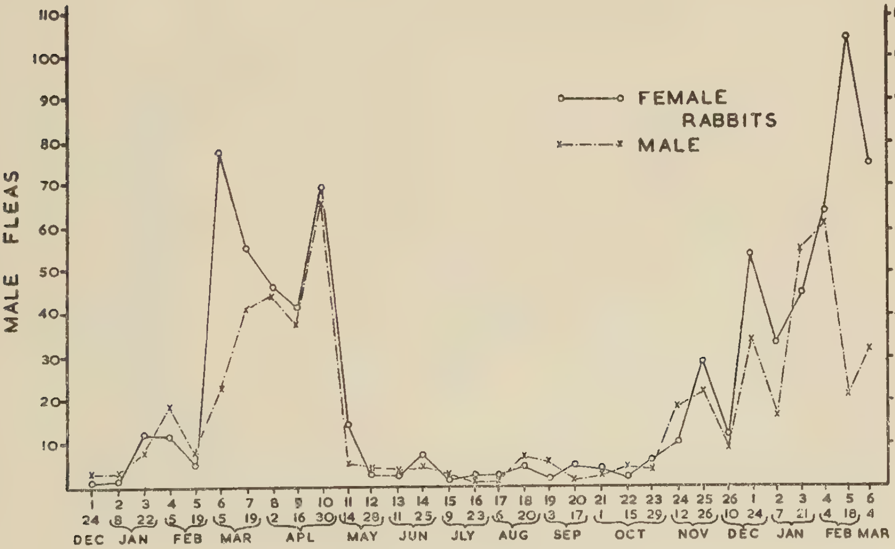

Fig. 2.—Average number of male fleas per rabbit.

between the rabbit sexes. There is then a sudden drop in the flea population. The remaining fortnights show relatively small fluctuation.

Figure 2 shows the average number of male fleas per rabbit and also the average for male rabbits and female rabbits separately. (As in fig. 1, only the values for male and female rabbits are plotted.) This gives similar results to figure 1.

Owing to the great difference in total number of fleas over the range of fortnights it is not possible to compare the percentage male fleas for all the counts made but it is possible to take fortnights 6–10 and compare the percentage male fleas for these fortnights (fig. 3). Assuming that the peak at fortnight 6 is an emergence peak, there is no evidence that the male flea dies off more quickly than the female, in fact from the graph there a is slight indication that the opposite may be true.

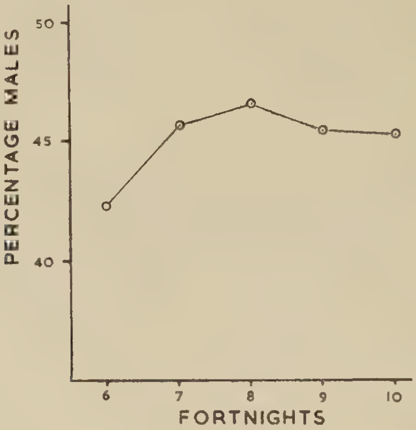

Fig. 3.—Percentage of male fleas per fortnight.

At certain times of the year fleas were to be found on the head and body, although by far the greatest population was present on the ears, usually among the hairs on the inner surface of the ear near the tips (fig. 4). The fleas from the ears represented 79·4 per cent. of the total infestation for all fortnights. The peak body population occurred at fortnight 3 (22.i.54), where the body gave 71·45 per cent. of the total. A gradual decrease then took place until by fortnight 6 (5.iii.54) fleas were to be found on the ears only.

A number of fleas were obtained from the head, mainly during fortnights 4 and 5 and also to a lesser extent during the summer months. The peak of activity occurred at fortnight 4 (5.ii.54), where 49·83 per cent. of the total fleas were from the head. Further studies of the populations conducted during 1955, although terminated by the appearance of myxomatosis after only six sets of data, show a remarkable correspondence with the previous year. There is the same increase in fleas on the female rabbit on 18.ii.55, which corresponds to the similar increase in the previous year of 5.iii.54, both these being followed by a drop in the number of fleas on female rabbits. Very similar results are also recorded in the distribution of the flea on the host's body. It is apparent that the fleas were present earlier in 1955 than in the previous year, perhaps due to climatic conditions.

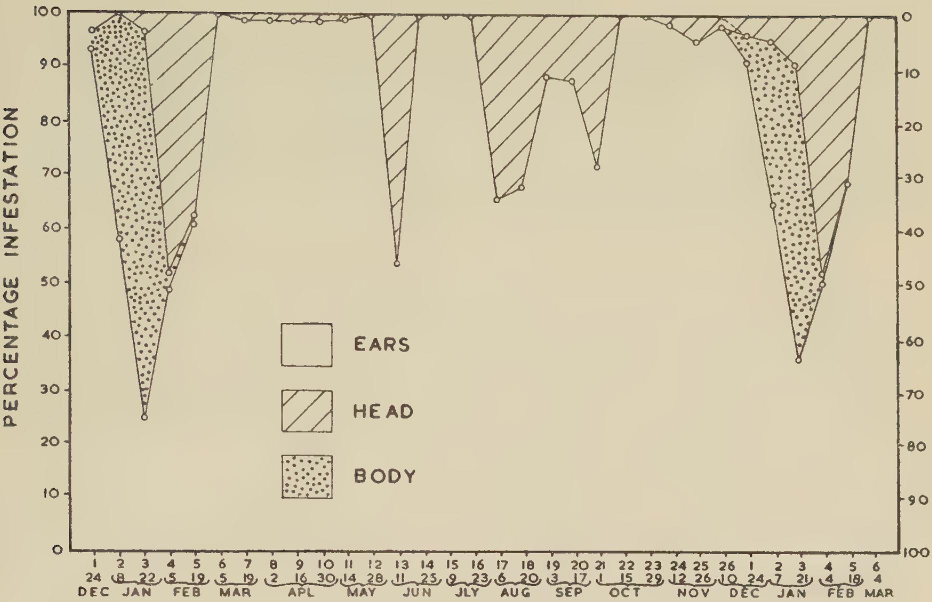

Fig. 4.—Percentage of fleas on ears, head and body per fortnight.

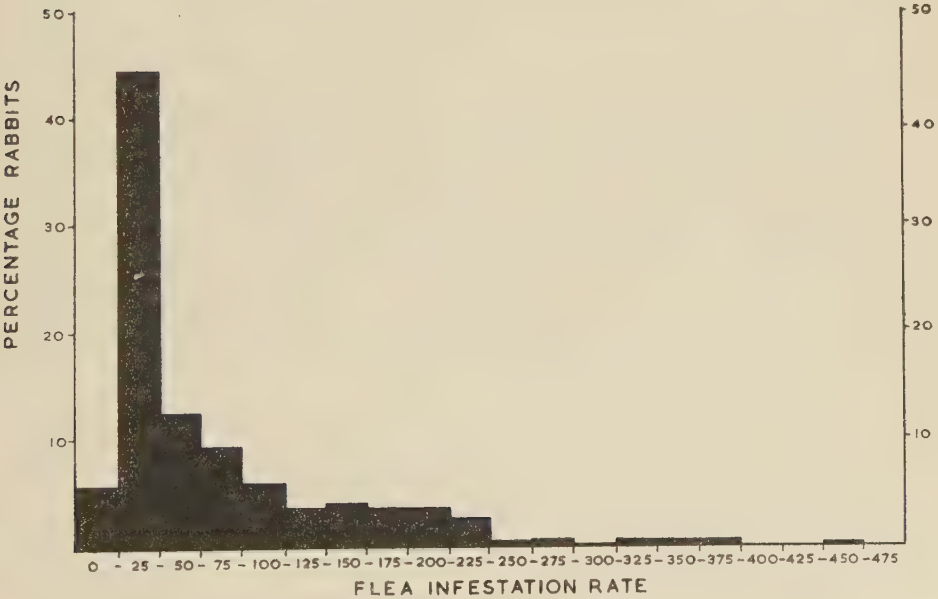

Fig. 5.—Infestation rate per rabbit.

A total of 640 rabbits was examined during the whole study. Of these 5·63 per cent. had no fleas whatever (fig. 5), these parasite-free rabbits being found almost entirely at the time when the flea population was generally low. Most rabbits (44·69 per cent.) had between 1 and 25 fleas on them and very few had more than 225 at any time of the year. The two highest populations recorded were 427 and 430; these high infestations were found on 19.iii.54 and 4.iii.55 respectively, both from female rabbits.

Discussion.

It has been established that the flea *Spilopsyllus cuniculi* occurs on the wild rabbit at all times of the year, and that there is a significantly higher population in March and April than during the remainder of the year.

It will be noticed that there was a higher total population during 1955 than in 1954. This may be caused by one of two reasons : either the previous season had been climatically more suitable for the breeding of the flea or rabbits were more scarce. In view of the fact that 17,000 rabbits had been marketed from the Ballogie area during 1954, the latter may be true, although extensive rabbit control had been exercised there for some time. It should be appreciated that a smaller host population does not necessarily mean there will be an increase in the number of fleas on the remaining rabbits. This may only be true if the previous season was specially favourable for the larval stage of the parasite and there were the same number of hosts or fewer available for the adult fleas on emergence. In view of the probability that the rabbits marketed from Ballogie shed fleas far from rabbit warrens it is more difficult to understand how the increase during the second year occurred. In experiments carried out on the Heisker or Monach Islands, Outer Hebrides (Shanks *et al.*, 1955), the rabbit fleas present died out, or at least became extremely scarce there, after the presence of myxomatosis considerably reduced the rabbit population on these islands.

During the first week of March only the adult female rabbit had a high rate of infestation. It would appear probable that at this time of year the pregnant doe rabbit searches the old stops, which have not been incorporated with the main warren, for a suitable place to rear her young. In doing this, the doe may disturb fleas lying dormant in the pupal stage. It is well known that fleas may remain in the pupal stage for many months if left undisturbed but will emerge in response to vibration or warmth. It is probable, therefore, that it is in this way that the increase of fleas on doe rabbits is made. This is corroborated by Southern (1940). Two observations are of interest in this connection. Firstly, from fig. 4 it can be seen that at the time when one would expect the doe rabbit to be concerned with finding her stops, an increase of fleas occurs on the body (fortnight 3). This rise in population is next apparent on the head (fortnight 4), finally settling on the ears (fortnight 6), where they remain for the remainder of the breeding season of the rabbit. The same trend occurred during the second series of counts (1955). Secondly, gravid female fleas were only to be found during fortnights 8–13, the period when one would expect the nest of the doe rabbit to be occupied by her young.

Rabbit fleas kept unfed in a refrigerator at 20° F. were still alive after a period of nine months and became quite active when exposed to warmer temperatures. Sections of these indicate that there was only a small reserve of fat body present at the end of this period. In the field, fleas have been kept alive in a vacated rabbit warren for 70 days without food and for an even longer time on rabbits in an outside run. A wild rabbit was caught during April, 1955 and had at that time an abundance of fleas on its ears. Unfortunately this rabbit died during the summer of that year and a domestic rabbit was immediately put in the run, the fleas from the dead wild rabbit being allowed to attach themselves to their new host. At the time of writing (31.i.56) there are still nine fleas attached to the ears of the tame rabbit.

CONCLUSIONS.

From the above observations it is, in the opinion of the author, possible to give a tentative life history of the flea.

The eggs are laid, probably indiscriminately, by the gravid female and those which happen to be deposited in the nest of the rabbit develop into larvae which, after an unknown time, pupate in the stop of the doe rabbit. The following spring, when the rabbit enters the stop, it becomes infected with fleas which have either hibernated in the nest or are stimulated to emerge from the pupae by the disturbance caused by the rabbit. These climb on the rabbit's body at first but finally settle on the ears. After a period of feeding, the female fleas become gravid, laying their eggs during the breeding season of the rabbit. Probably the majority of these fleas are relatively short lived, although some may live for several months ; it is also possible that, after feeding, numbers leave the body of the host and remain in the nest, or may even pass the winter in hibernation. As one would expect, the life history of *Spilopsyllus cuniculi* is closely linked with that of the rabbit.

OTHER PARASITES.

During the investigation several other rabbit parasites were found. From the 640 rabbits examined only four sheep ticks, *Ixodes reduvius* L., were found. These were obtained during the spring of 1954. Ballogie being a hill area, one would have expected a higher proportion of ticks on the rabbits.

Harvest mites, *Trombicula autumnalis* Shaw, were obtained on several occasions, mainly during January and February, 1955. These were attached to the ears and were feeding in company with the fleas. At no time during the survey were lice encountered.

A myxomatosis infected rabbit with three specimens of the black fly, *Simulium reptans* L., was found near Ballogie during late June, 1955.

SUMMARY.

A tentative life-history of the flea *Spilopsyllus cuniculi* (Dale) is given, with notes on the habits of the adult fleas and the results of 15 months' field work on the populations of the flea on wild rabbits in north-east Scotland, where the insect is the chief vector of myxomatosis. The fleas were sexed and the numbers and sites of each sex on the rabbit are recorded. Most rabbits were infested, some carrying more than 400 fleas.

ACKNOWLEDGMENTS.

The writer is indebted to Lt.-Col. J. W. Nicol, D.S.O., of Ballogie, the owner of the Estate, for his kind permission to carry out the observations and to Mr. Low, the head keeper, for his assistance and consideration during the field work. The assistance of the Statistical Department of the University of Aberdeen in analysing the results is also acknowledged. The author would like to thank the Hon. Miriam Rothschild for her assistance throughout the investigation and also for criticising this manuscript.

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THE COURSE OF OXYGEN CONSUMPTION DURING THE MOULTING CYCLE OF *RHODNIUS PROLIXUS* STÅL (HEMIPTERA).

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During the pupal stage of insects the rate of metabolism as measured by the oxygen consumption, the carbon dioxide production or the generation of heat follows a U-shaped curve : it first falls to a low level and then rises to a peak at the time of emergence of the adult. (For references *see* Edwards (1953) and Wigglesworth (1953*a*)). Preliminary results (Edwards, 1953) suggest that the same type of curve occurs during the moulting cycle of the hemimetabolous bug *Oncopeltus*.

In the hope of throwing further light on the significance of this curve the oxygen uptake during the moulting stages of *Rhodnius* has been studied and the findings related with the histological changes taking place at each point in the cycle. *Rhodnius* is particularly well suited to studies of this kind because growth is initiated by a single large meal of blood and ecdysis takes place at a fairly constant interval after feeding.

METHODS.

The measurements were made on single insects in differential manometers of Barcroft type. The larvae were placed in stainless steel cages lined with filter paper over 20 per cent. potassium hydroxide to absorb carbon dioxide. Oxygen consumption, usually at 25° C., was measured over a period of about 10 hours and expressed in cubic millimeters of oxygen per hour per insect. There was evidence that growth did not proceed normally if the insects were kept permanently in the manometer vessels for many days. In most experiments, therefore, large batches of insects were fed and different individuals were used to determine the average oxygen consumption at a given day.

Methods of studying the histological changes in the tergites and sternites of the abdomen in *Rhodnius* have already been described (Wigglesworth, 1933, 1947, 1953*b*).

OXYGEN UPTAKE DURING MOULTING.

Figure I shows the general course of oxygen uptake in third, fourth and fifth stage larvae of *Rhodnius*. The interrupted segment of the curve represents the period of indefinite duration between feeds ; this may be a week or ten days, or it may be several weeks. Figure 2 gives in detail the course of oxygen uptake in the fourth stage larva at 25° C. and at 30° C. In these experiments the insects at 30° C. took fourteen days to moult ; as a rule fourth stage larvae at this temperature require only eleven or twelve days between feeding and moulting.

The oxygen consumption in the unfed insect is at a low level. After feeding it rises steeply and, at 25° C., continues to rise for five or six days, reaching a

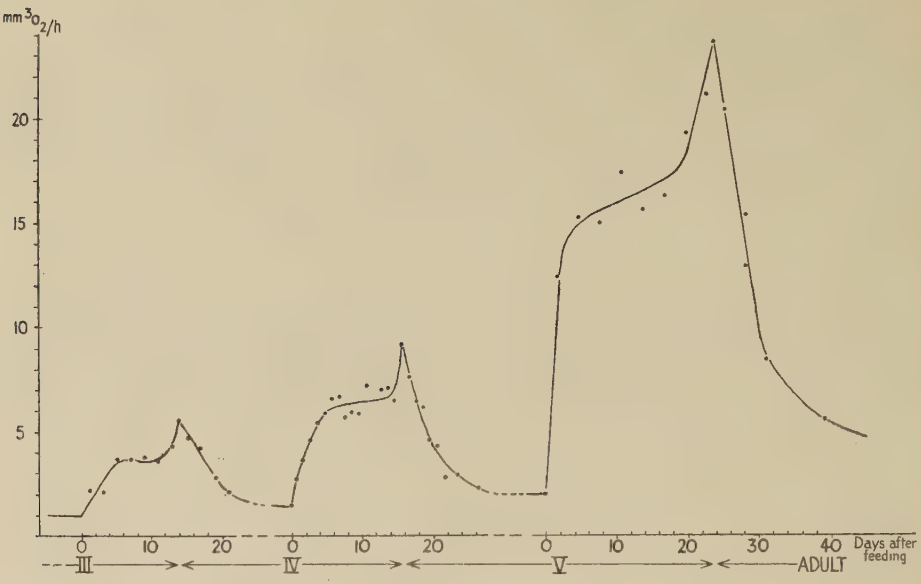

FIG. 1.—Oxygen uptake during moulting in third, fourth and fifth stage larvae of *Rhodnius* at 25° C. *Ordinate:* oxygen consumption in mm.³ 0_2/hr. *Abscissa:* days after feeding.

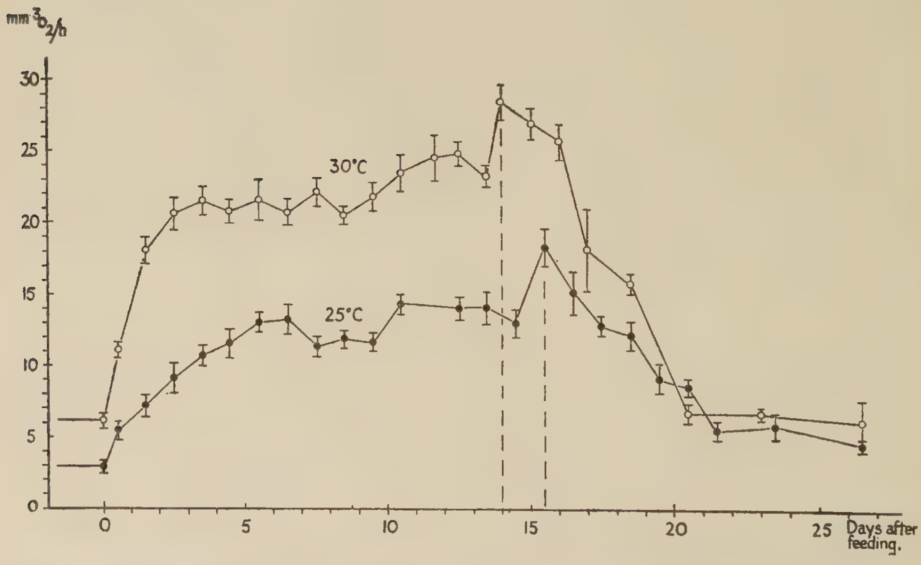

FIG. 2.—Oxygen uptake during moulting in fourth stage larvae of *Rhodnius* at 25° C. and 30° C. *Ordinate:* oxygen consumption in mm.³ 0_2/hr. *Abscissa:* days after feeding. The vertical broken lines mark the time of moulting.

level four or five times that of the resting insect. Thereafter, apart from some fluctuations of doubtful significance, the level remains more or less constant, perhaps rising slightly, until the day of moulting when there may be a conspicuous peak. After moulting the oxygen uptake falls steadily for about five days and then settles down to a resting level which is about one-third of that during the preceding moulting period.

Thus the curve of respiration in *Rhodnius* shows a series of peaks during the latter part of the moulting cycles and a series of depressions between moults. If that part of the curve which extends from one ecdysis to the next is considered alone, it follows roughly a U-shaped course. That is probably the significance of the U-shaped curve during the pupal stage of insects: the descending segment of the curve represents the fall from the peak level of the preceding moult, and the ascending segment the rise to the following peak.

But we must now consider what changes are responsible for the course of this curve.

HISTOLOGICAL CHANGES DURING MOULTING.

The changes during moulting have been observed only in the epidermis, muscles, fat-body, etc. of the abdomen; but these changes probably provide a sufficient indication of what is happening elsewhere. They will be described in the fourth stage larva at 25° C.

During the first few hours after feeding there is a rapid elimination of perhaps three quarters of the fluid in the ingested blood (Wigglesworth, 1931). Then digestion and absorption, and the excretion of waste products, particularly of uric acid, proceed continuously for more than 28 days: red undigested blood is still present in the " stomach ", the dilated first segment of the mid-gut, until more than ten days after moulting to the fifth stage. It therefore seems unlikely that the curve of oxygen uptake is related with digestion and absorption; it is probably connected with the processes of growth.

The epidermal cells are becoming conspicuously " activated " within forty-eight hours after feeding (Wigglesworth, 1934); that is, the nuclei and particularly the nucleoli become enlarged and the cytoplasm dense and deeply staining. By four days after feeding, mitoses in the epidermis are beginning; they usually reach their peak at six days and are complete by the seventh or eighth day.

Deposition of the epicuticle begins on the seventh or eighth day and from then on the epidermal cells assume a high columnar form as the chitin and protein of the inner layers are formed (Wigglesworth, 1933).

In the course of this work we have found that, before the epidermal cells become detached and begin to lay down the new cuticle, they add more chitin and protein to the inner layers of the old cuticle. In dissecting the insects it is evident that the cuticle of the abdomen becomes firmer and more rigid during the first few days after feeding. Figure 3 shows that by the sixth day after feeding about 30 per cent. has been added to the thickness of the cuticle. Then follows the formation of the new cuticle and the digestion of the old. After moulting, secretion of the endocuticle continues. Indeed, the inner third of the entire cuticle is laid down during the first four days after moulting (Wigglesworth, 1933). Thereafter the formation of cuticle gradually comes to an end as the food reserves are used up, and the epidermal cells become attenuated once more (Wigglesworth and Gillett, 1936).

The fat body increases its stores of fat, protein and glycogen during the moulting period. These increase particularly after the seventh day; in the later days of moulting, protein and glycogen are transferred to the epidermis and elsewhere (Wigglesworth, 1947). This build-up of reserves is preceded by active growth and mitosis in the fat body cells, which begins about the fourth day and ends about the ninth day after feeding.

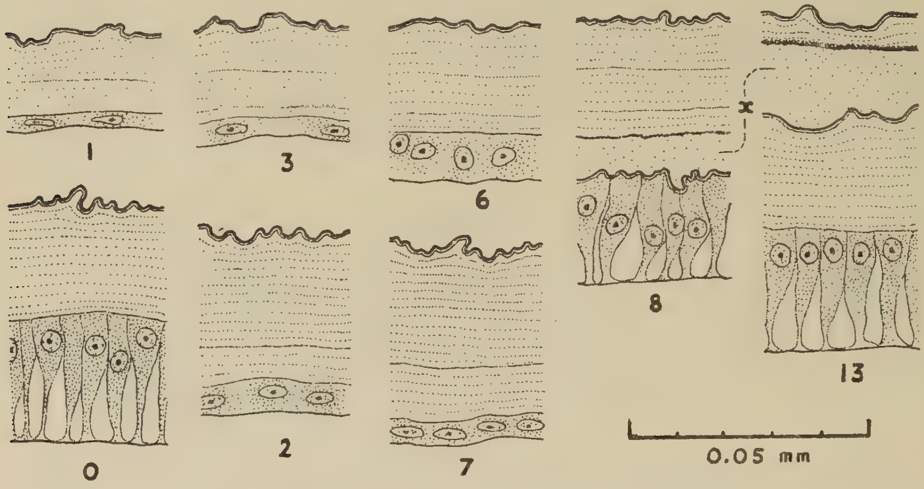

FIG. 3.—Transverse sections through the integument of fourth stage and fifth stage larva of *Rhodnius* at different periods in the moulting cycle. 1, one day after feeding; 3, 6, 8, 13, three, six, eight and thirteen days after feeding. 0, fifth stage larva on day of moulting (fourteen days after feeding); 2, 7, two days and seven days after moulting. *x*, indicates the moulting fluid between the old and the new cuticles.

The haemocytes increase progressively in numbers from the day of feeding until at least the ninth day (Wigglesworth, 1955).

In the abdominal muscles there is a remarkable cycle of growth which will be described in full elsewhere (Wigglesworth, 1956). Briefly it may be said that the intersegmental muscles on the tergites of *Rhodnius* are almost completely vestigial. The muscles of the sternites are well developed but they are functional only during the act of moulting. Thereafter the muscle fibres degenerate and within four or five days after moulting nothing remains of the muscles except a connective tissue sheath containing the muscle nuclei, now almost devoid of cytoplasm. The new muscle fibrils begin to appear within a day or two after feeding, but development is not complete until a day before moulting.

INTERPRETATION OF THE COURSE OF OXYGEN CONSUMPTION.

The first point to note is that there is no evidence of particularly active oxygen uptake during the period of mitosis which extends from about the fourth to the eighth day after feeding. That agrees with the findings of Tuft (1953) on respiration during embryonic development in *Rhodnius*.

The process which is most clearly associated with oxygen consumption is the synthesis of protein. During the first five days after feeding there is a build-up of cytoplasm in the epidermal cells everywhere, followed by a great increase in cell number. Then follows a period of steady formation of the protein and chitin of the endocuticle ; and throughout this whole period the protein of the muscle fibrils is being laid down.

When the cuticle is shed there are special processes, such as the muscular activity required for the actual ecdysis, and the subsequent darkening and hardening of the new cuticle, which are presumably responsible for the peak of oxygen uptake often observable at this time.

Protein synthesis for the cuticle continues at a decreasing rate during the first few days after moulting and is presumably responsible for the descending part of the curve.

According to this interpretation, the curve of oxygen uptake during the moulting stages in *Rhodnius*, and perhaps during pupal development in other insects, is primarily a curve of protein synthesis. As is well known, protein synthesis is an endothermic process making large demands for energy.

EFFECT OF DECAPITATION, CYANIDE, ETC.

If the fourth stage larva of *Rhodnius* is decapitated at one day after feeding, so that moulting is prevented, the oxygen uptake continues to rise for a few days and then falls towards the resting level.

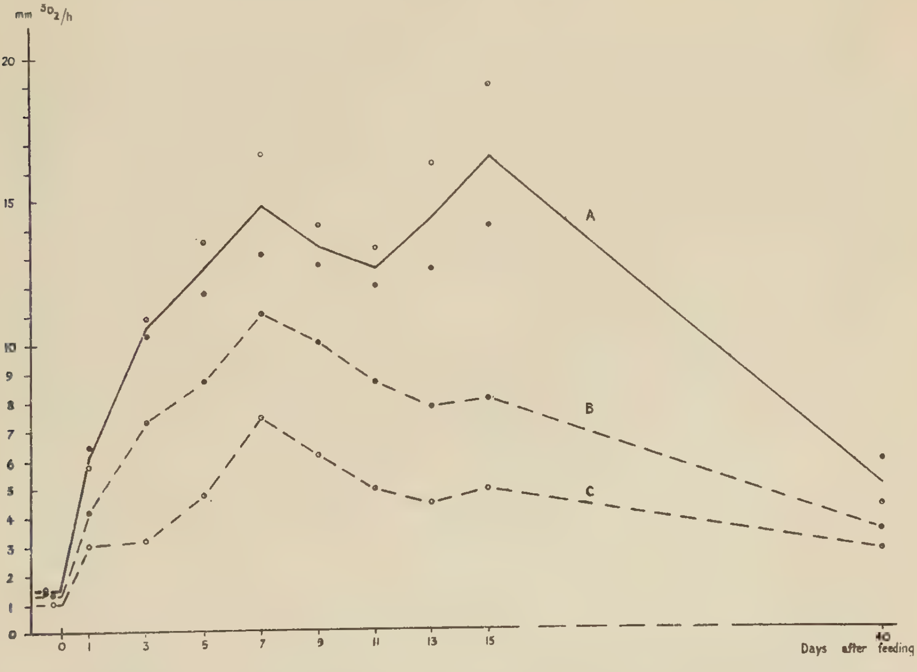

FIG. 4.—Effect of two concentrations of cyanide on the oxygen uptake of fourth stage larvae of *Rhodnius* at different stages of the moulting cycle. *Ordinate :* oxygen consumption in mm.^{3} 0_2/hr. *Abscissa :* days after feeding. A, controls. B, exposed to $1 \cdot 3 \times 10^{-4}$M cyanide. C, exposed to $2 \cdot 8 \times 10^{-4}$M cyanide.

Finally, a few observations have been made on the effect of cyanide. In these experiments the potassium hydroxide was replaced by Robbie solution ($Ca(CN)_2$ in $Ca(OH)_2$ with undissolved $Ca(OH)_2$ in excess). This solution absorbs the carbon dioxide and at the same time keeps the atmosphere in the flasks at a constant cyanide level. The concentrations used were 0·3M and 0·6M, corresponding to about $1{\cdot}3 \times 10^{-4}$M and $2{\cdot}8 \times 10^{-4}$M in the gas phase. The cyanide concentration in the solutions was determined by Liebig's method; the corresponding gas values were taken from the chart in Robbie and Leinfelder (1945). All-glass receptacles were substituted for the steel cages. Two batches of insects were used, one for each concentration. The oxygen uptake of samples of each group was measured first in air and the following day in cyanide.

The results are insufficient to calculate the basic cyanide-stable respiration. But in all the experiments the curves (fig. 4) showed a change in the relative amount of cyanide-sensitive respiration: at both concentrations of cyanide the curve of oxygen uptake falls continuously after eleven days, whereas the total respiration of insects in air rises to a peak at moulting. It would seem that the cyanide-sensitive respiration increases continuously up to the time of moulting, whereas the cyanide-stable part increases at first and then falls towards the time of moulting. This would suggest that the cytochrome system (the most important component of the cyanide sensitive respiration) becomes relatively more important during the final stages of moulting.

Discussion.

During the pupal stage of insects the muscles and other organs peculiar to the pupa suffer histolysis and this is followed by histogenesis of the organs of the adult. It is not surprising, therefore, that the total quantity of respiratory enzymes present in the tissues should follow a U-shaped curve of the same general form as the curve of oxygen consumption during the same period. That has been shown to be so for the Warburg-Keilin system in *Drosophila* (Wolsky, 1938; Bodenstein and Sacktor, 1952), *Musca* (Sacktor, 1951), *Vanessa* (Schwan, 1940) and *Platysamia* (Williams, 1950), and for the substrate-dehydrogenase systems in *Drosophila* (Wolsky, 1941), *Vanessa* (Schwan, 1940) and *Calliphora* (Agrell, 1947).

Active tissues with a high demand for oxygen naturally have a correspondingly large supply of respiratory enzymes. But the level of oxygen consumption is determined, not by the quantity of oxygen carriers present, but by the functional activity of the tissues. That is very evident in an insect like *Rhodnius* with a large amount of muscle, immensely rich in cytochromes, which persists from one stage to the next. It is possible to demonstrate the influence of growth and moulting on the uptake of oxygen in *Rhodnius* only because the larvae remain practically motionless in the manometer chambers and therefore the abundant cytochrome system in the muscles is inactive.

Indeed, even in insects which have little persistent muscle, the curve of oxygen consumption may not agree at all closely with the curve for the amount of cytochrome oxidase. That is so, for example, in the pupa of *Bombyx mori* (Ito, 1955); and in the egg of *Melanoplus* the cytochrome oxidase increases as the mass of the embryo and is not correlated with the curve of oxygen uptake (Bodine and Boell, 1936; Allen, 1940).

It has been noted by several authors that the calorific quotient (the ratio of oxygen consumed to heat produced) is extremely low during pupal development (Balzam (1933) on *Bombyx* and *Lymantria*, Taylor and Crescitelli (1937) on *Galleria*). This was attributed by Balzam to endothermic reactions associated with growth. Now that it is realised that protein synthesis, which is the chemical change most characteristic of growth, is an endothermic process, it is reasonable to ascribe to this both the low calorific quotient, and the U-shaped curve of respiration during the moulting cycle. Oxygen uptake rises to a peak along with the formation of new tissue before ecdysis and falls again as the formation of new tissue comes to an end during the next few days.

Summary.

In the larval stages of *Rhodnius* the uptake of oxygen rises during the first few days after feeding (at 25° C.) to a level about four or five times that of the fasting insect. The level remains more or less constant during the next few days, but rises to a peak during the day when ecdysis occurs (13–15 days after feeding, in the fourth stage). It then falls towards a new resting level during the next few days.

This curve of oxygen consumption is regarded as being in the main a curve of protein synthesis ; that is, increase in cytoplasm and in cell number, formation of muscle fibrils and formation of chitin and protein in the cuticle. It is compared with the U-shaped curve of respiration during the pupal stage of holometabola, which may perhaps have a similar explanation.

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THE IDENTIFICATION AND DISTRIBUTION OF THE LARVAE OF SOME SPECIES OF *CHIRONOMUS* (DIPTERA).

By A. B. Acton.

The identification of members of the genus *Chironomus* is made difficult by the fact that specific names can at present be given to male imagines only, and, in general, females and immature stages are unidentifiable. Though, for reasons of expediency, external morphological characters are used almost exclusively in taxonomy, it may sometimes be necessary to use any other characters which may be available. The larvae of Diptera possess giant chromosomes the banding-pattern of which provides a means of identification which is unique.

It has been suggested by Bauer (1945) that cytological features could be used, either alone or in conjunction with previously accepted criteria, to provide a means of identification of the Chironomidae. The method he suggests makes use mainly of the grosser features of the giant chromosomes, and has the advantage that the morphology of the chromosomes will not be subject to short-term fluctuations conditioned solely by the environment, or in general by the age of the larva, but is, of course, subject to evolutionary change. As Bauer has pointed out, the morphology of the chromosomes does not stand in any direct functional relationship to the immediate activities of the animal, and there will consequently be no selection to produce similar chromosome banding-patterns as the result of the fact that different species occupy similar habitats. Therefore convergencies, which so often obscure a natural classification, will be of much reduced importance, and it is in the chromosomes that evolutionary changes will be most faithfully reflected.

If drawings are made of the salivary-gland chromosomes of larvae these will provide a usable criterion of the species to which they belong, provided certain chromosome rearrangements which may occur are taken into account. All populations of *Chironomus dorsalis* which have been studied have included a number of individuals with parts of their chromosomes inverted. Between widely separated populations of this species there may (*unpublished*) be a difference in banding-pattern which, if not understood, might give the impression that such populations were non-interbreeding. These inversions are inherited unchanged and seem to be in no way a bar to fertility. Differences of this nature cannot, of course, be used as species criteria, and there will probably be no system in which judgments of value become unnecessary.

The chromosomes of *C. tentans* and *C. pallidivittatus* have patterns which differ in the main by a number of inversions. It is possible to mate the two species under laboratory conditions and to raise fertile hybrid-imagines (Beermann, 1953). Beerman found, however, that there was a considerable reduction in the viability of the eggs in the species-cross and it might be expected from this that when the species occur together in the same pond they will produce few viable hybrids ; I have, in fact, found this to be so. In a combined sample from a single pond containing 995 *C. tentans* and 41 *C. pallidivittatus* larvae there was one first-generation hybrid and three " partial " hybrids in which only one or two of the eight chromosomes were *C. pallidivittatus*. The slight morphological differences between the imagines (*see* Coe 1950) and the reduced interfertility suggest that these are indeed good species.

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C. dorsalis, *C. thummi*, *C. tentans* and *C. annularius* have been found together in various combinations in the same pond and, though a hybrid between any pair of these species could easily be identified by its giant-chromosomes, I have not seen one. The numbers examined are high enough to suggest that such hybrids are either very rare, or are never formed. *C. tentans* larvae were sent to Germany and the imagines which emerged were mated by Beermann (Beermann 1955*a*) with imagines from Sweden. Imagines from Sweden were also crossed with those from Germany, and all matings proved to be fertile. The identifications were based on chromosome banding-patterns and the fact that the imagines produced fertile offspring confirms both that the confidence which was placed in the chromosomal method of identification was justified, and also that basically identical banding-patterns usually imply complete interfertility.

Drawings were made of the salivary-gland chromosomes of all the species named in this paper and, in addition, those of three of these, *C. thummi* (Bauer (1935), *C. tentans* and *C. pallidivittatus* (Beermann 1955*b*), have already been published so that a means of comparison is available. To be able to study life-histories and ecological relationships it is obviously essential to know firstly what the species is, but, more important, whether it is the same species throughout which is being studied. It has, for instance, been reported (Stuart 1941) that *C. dorsalis* occurs in shore pools and that the larvae will survive in a 25 per cent. concentration of sea-water. This report is of some ecological interest, especially as the larvae of this species appear, by the fact that they very often do not occur in ponds in which other species are found, not to be able to colonise all fresh-water ponds. However, the basis of this report is the identification of imaginal material and it is perhaps not surprising that the description which is given of the larva does not correspond with that of *C. dorsalis*, being, in the first place, of the *thummi* and not the *plumosus* group, and also differing in the shape of the mandibles. It is likely, then, that these larvae were incorrectly identified, not by error, but because of the limitations of the system used, and most, if not all, the interest of the original observation is lost. Where the chromosomal method of identification is used there can be little doubt.

Two important papers on the taxonomy of this group are those of Edwards (1929) and Coe (1950). In these *C. dorsalis* and *C. thummi* (= *C. riparius*) are stated to be common in the British Isles. This has been supported by a study of the giant chromosomes of larvae from ponds and lakes in England and Scotland. *C. dorsalis* and *C. thummi* are known to occur also (chromosomal identification) in Germany (Bauer 1935, 1936) and Austria (Mainx, Kunze and Koske, 1953) and, further, a comparison of chromosomal preparations has shown that *C. annularius* occurs in Germany (Beermann, 1955*a*). These observations may seem to be superfluous, but it should be remembered that there is, at least with *C. dorsalis* and *C. thummi*, some doubt as to the validity of the taxonomic characters now in use (Acton, 1955). The widespread distribution of these two species is therefore well established, and it is of interest that C. *dorsalis* has been reported in Japan (e. g. Tanaka, 1939), but whether this is the same species, in the sense that interbreeding is possible, as the one found in Europe cannot be stated as certain.

C. annularis, *C. tentans* and *C. pallidivittatus* are reported by Edwards and

Coe from a limited number of localities only in the British Isles. Reports of this nature depend entirely, of course, on the extent of the collections on which the reports are based, but, as these have remained little altered for over 25 years, there is some reason to believe that the species are, in fact, uncommon. However, larvae of *C. tentans* and *C. annularis* have been taken from a number of ponds, which shows that their distribution is as widespread as that of any of the other species just mentioned. The larvae of *C. pallidivittatus* were found in one place only (Sheepstead), in small numbers together with those of *C. tentans*. *C. pallidivittatus* has been found by Beermann (1955*b*), also in small numbers together with *C. tentans*, in Germany. The larvae of *C. tentans* have been found in Sweden by the same worker. Thus, though *C. pallidivittatus* may be rare, the very closely related *C. tentans* most certainly is not.

No external features could be found which would serve to identify the species to which the larvae examined in this work belonged. Nevertheless, where certain combinations of species alone are considered, these can be differentiated with some confidence (Table I). The larvae of *C. dorsalis* and *C. thummi* are easily distinguished by the extra pair of lateral appendages in larvae of the former species (*plumosus* group). The head of *C. dorsalis* larvae is unpigmented except for the extreme posterior edge. In *C. thummi* the pigmentation extends to the ventral plates, but this is never dense or extensive. The larvae of *C. annularius* (*plumosus* group), and at least one other species, have extensive pigmented regions on the ventral head plates, but in small, though mature, larvae these may be very lightly coloured and in a very few cases not distinguishable from those of *C. dorsalis*. These, in turn, can be distinguished almost without exception from the larvae of *C. tentans* and *C. pallidivittatus*, which have a conspicuous wedge-shaped mark on the dorsal surface of the head. The apex of the wedge points to the rear and the pigmentation extends forward to the front of the head. (This character was first reported by Thienemann in a paper by Beermann (1952)).

TABLE I.—*Some morphological features of different species of* Chironomus *larvae.*

	Pigmentation on head.	Lateral appendages.	Numbers on which this observation is based.
C. dorsalis	Posterior border only	Yes	680
C. thummi	Post. border + ventral plates ; never dense	No	68
C. annularius	Post. border + ventral plates ; usually dense, sometimes pale	Yes	82
C. tentans	Post. border + ventral plates + wedge-shaped mark on top of head ; rarely absent	Yes	2280
C. pallidivittatus	As above	Yes	41

A sample of larvae taken from a pond was classified cytologically and found to belong to a number of species. These were *C. dorsalis*, *C. annularius* and three unidentified species, one of the *plumosus* group and two of the *thummi* group, but neither *C. tentans* nor *C. pallidivittatus* were present. The larvae of one of the unidentified species had a dark wedge-shaped mark on the head similar to that of the two last-named species. However, while the larvae of

C. tentans and *C. pallidivittatus* belong to the *plumosus* group, those of the unidentified species, in which the banding-pattern of the chromosomes is quite distinct, were all of the *thummi* type. This observation stresses the need for careful identification, especially when the controversy as to whether a given species has larvae of one type only is involved. In view of the numbers which have been examined (Table I), there can no longer be any doubt (*see* Acton, 1955) that larvae of a given species belong to one group only. Though the characters described above cannot be used as absolute species criteria, they are for some purposes extremely useful, and may serve as a basis for further work.

SUMMARY.

A method of identification of larvae of *Chironomus* using the banding-pattern of the giant chromosomes is discussed. In view of the doubt as to the validity of the taxonomic characters used in some cases, the widespread distribution of *C. dorsalis* and *C. thummi* is confirmed by cytological methods. By the same method it has been shown that *C. tentans* and *C. annularius* are not as uncommon in the British Isles as previously reported, unlike *C. pallidivittatus* which appears to be rare. Some of the morphological features of the larvae of these species are described.

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A SUPPLEMENTARY NOTE ON *PROSOPISTOMA* LATREILLE (EPHEMEROPTERA).

By M. T. Gillies.

In a recent publication (Gillies, 1954), I gave a general account of the genus *Prosopistoma* Latreille with special reference to the morphology of both adults and nymphs. The description of the former was based on a series of imagines and subimagines of a new species from East Africa, *P. africanum.* No imagines of *Prosopistoma* had previously been described, but within six months of the publication of my account the imago of the well known European species, *P. foliaceum* (Fourcroy), was described independently by two French workers, Fontaine (1955) and Degrange (1955). Their accounts show that the adults of both species are very similar. The object of the present note is to comment on the few differences reported and also to provide an additional point of information on the gills of the African nymphs.

Wing Venation in the Male.

Degrange records the presence of 14 main veins in the male wing, rather than the 13 depicted by Fontaine and myself. His figure shows these 14 veins together with two additional veins terminating on the inner border of the wing. Re-examination of a series of *P. africanum* males has shown that in this species also there is a single concave vein running alongside and parallel to the internal wing margin. I had previously mistaken this vein for the folded back margin of the wing—in dry wing mounts a slight degree of folding of the margin often occurs—and in my previous publication no mention was made of it. The wing of the male *P. africanum* is accordingly re-drawn here (fig. 1).

Degrange suggests that all the main veins are represented in the male wing,

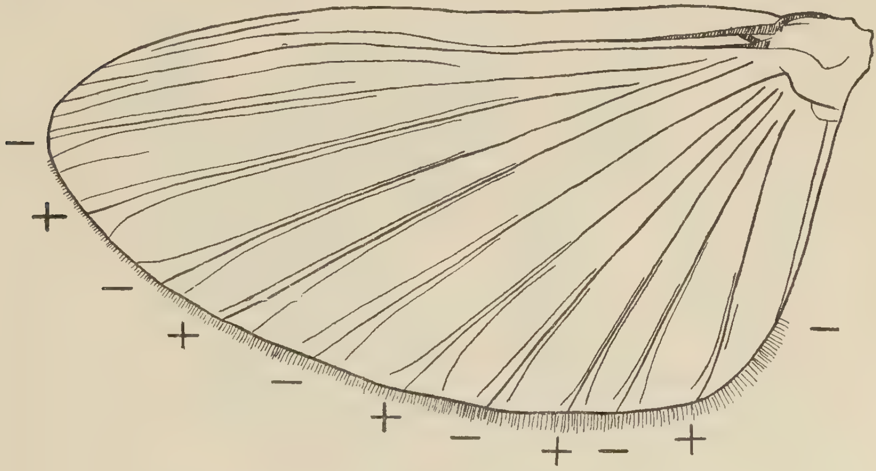

Fig. 1.—*Prosopistoma africanum* Gillies. Male fore wing.

and, if one accepts his interpretation of their homologies, then the most posterior vein in *P. africanum* is CuP(—), while in *P. foliaceum* it seems that the anal vein is present as well. The final concave vein is much nearer the inner wing margin in *P. africanum* than in *P. foliaceum*, and the intervening space would seem to be too narrow to accommodate any additional veins such as Degrange has depicted. In his figure, also, the wing fringe is shown as extending beyond the concave CuP to as far as the termination of the next vein behind it. In *P. africanum* the fringe ends abruptly at the termination of CuP. This character has been found to be constant in a series of adults examined. There seems, therefore, to be some discrepancy between the two accounts here, unless these small but distinct differences are of a specific nature.

THE SIXTH NYMPHAL GILL.

In my previous account I stated that a sixth gill was only present in the Madagascar species, *P. variegatum* Latreille, and was absent in *P. foliaceum*, *P. wouterae* Lieftinck and *P. africanum*. This was incorrect. It is true that Vayssière (1882) described only five gills in *P. foliaceum* and that Lieftinck (1932) recorded the presence of five gills in the Malayan species, *P. wouterae*. But by mischance I overlooked the amended description of *P. foliaceum*, given by Vayssière (1890), in which the presence of a minute sixth gill was recorded. I was also unaware at that time of the recent publication by Mme. Fontaine (Lafon, 1952), in which the sixth gill was described and clearly figured.

Through the kindness of Mme. Fontaine, I have been able to examine some specimens of *P. foliaceum* and to observe for myself this minute gill. Re-examination of some specimens of *P. africanum* has revealed the presence of a similar tiny structure, not more than 0·25 mm. long, situated on the dorsum of the sixth abdominal segment. It may be described as a trumpet-shaped, rolled up chitinous plate, the lip of the trumpet being split open on one side to near its base. An almost identical and slightly larger gill has also been found in the South African species *P. crassi* Gillies.

Thus it appears that a sixth gill is present in every species in which it has been sought. It is possible that it exists in *P. wouterae* as well, but that, owing to its small size, its presence has been overlooked.

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TAXONOMY OF THE LARVAE OF THE BRITISH SPECIES OF THE SUB-FAMILY GLOSSOSOMATINAE (TRICHOPTERA).

By Mrs. Jean C. Mackereth.

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The family Rhyacophilidae is divided into two sub-families: Rhyacophilinae with four species in the genus *Rhyacophila*, the nymphs of which were described by Mackereth (1954); and Glossosomatinae with the following two genera and six species:

Glossosoma boltoni Curtis, 1834.
G. vernale (Pictet, 1834).
G. intermedia (Klapálek, 1892).
Agapetus fuscipes Curtis, 1834.
A. comatus (Pictet, 1834).
A. delicatulus McLachlan, 1884 (= *laniger* McLachlan, 1879 *nec* Pictet, 1834).

Klapálek placed the species *intermedia* in the genus *Mystrophora.* Kloet and Hincks (1944) showed that this name was preoccupied and erected the genus *Mystrophorella,* and Kimmins (1953) merged this with *Glossosoma.*

A. delicatulus has not been described before. Ulmer (1909) and Rousseau (1921) have described differences between *G. boltoni* and *vernale* and between *A. fuscipes* and *comatus. A. fuscipes* has also been described by Nielsen (1942) and Hickin (1943). Kimmins (1943) has described *G. intermedia.* Not all the differences mentioned by these authors have been found to be totally reliable on examination of further material, and it therefore seemed desirable to make a thorough comparative study of the six species. The results are now presented.

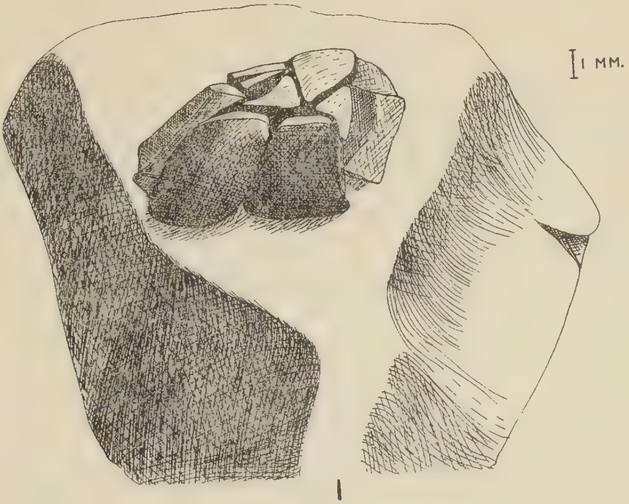


Fig. 1.—Pupal case of *Glossosoma intermedia* Klapálek.

The larvae are small and live in elliptical cases made of coarse angular sand grains. All the species are found in rapid stony streams or rivers, and *A. fuscipes* is also found in lakes. The larvae pupate in thin light-brown cocoons with the stone cases surrounding them on all sides except the under-surface which is attached securely to a large stone, as shown in fig. 1. Distinctions were established on cast larval skins recovered from the pupal cases after the adults had emerged. When good distinctions had been found from the cast skins, whole larvae were used.

Glossosoma boltoni Curtis.

Material: Hayes Water inflow CU, 1 cast skin, 13 whole larvae; Ford Wood Beck WL, 1 cast skin; Goldrill Beck CU, 1 cast skin; Holbeck WL, 1 cast skin, 1 whole larva; Pull Beck WL, 1 cast skin; Stock Ghyll WL, 6 cast skins, 7 whole larvae.

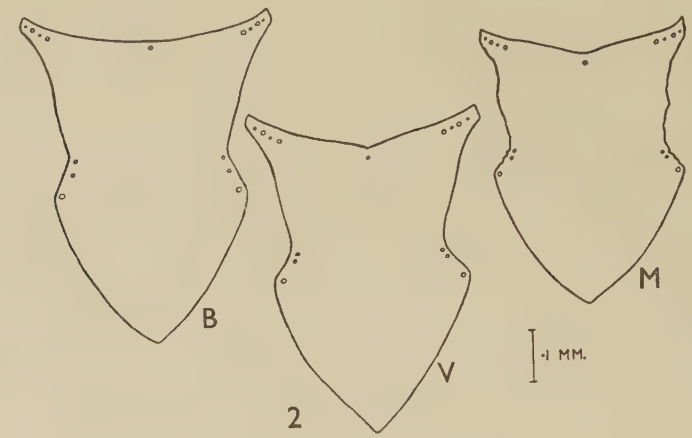


FIG. 2.—Fronto-clypeus: B, *Glossosoma boltoni*; V, *G. vernale*; M, *G. intermedia.*

Fully grown larvae from 8 to 10 mm. long and 1·5 to 3 mm. broad. Elliptical cases about 10 mm. long. The rounded head is dark brown and almost black in some specimens. Anterior edge of fronto-clypeus concave, as shown in fig. 2B. Pronotum also very dark brown, and with a single row of long black setae along the anterior edge and numerous setae posteriorly which are arranged in groups laterally. The band along the posterior edge is entirely black (fig. 3B).

No sclerotised patches present on the meso- or metanotum. Legs robust. Each claw with a single seta on the inner side arising from a short footstalk (fig. 4*b*).

Abdomen yellow or pinkish-yellow with short hairs arranged dorsally and ventrally on each segment. Anal claw short and robust, with one auxiliary spine attached to the outer edge.

The mandibles from the last larval skin, found in the pupal case, were all short, and very much as Ulmer and Rousseau depicted them, but the mandibles of newly moulted larvae were long and serrated. Nielsen states in his description of *A. fuscipes* that the claws and mandibles are longer than other authors have described them. It seems safe to surmise that the claws and mandibles get worn down as the larva crawls about and scrapes the stones for food.

Glossosoma vernale (Pictet).

Material: Black Beck WL, 2 cast skins ; R. Eden CU, 10 cast skins, 3 whole larvae.

Larvae and cases about the same size as those of *G. boltoni*. Both Ulmer and Rousseau distinguished *G. vernale* from *G. boltoni* on pigmentation of head and pronotum, *G. vernale* being yellowish-brown and *G. boltoni* dark brown. However, intensity of pigmentation was found to vary a good deal in the specimens examined and not to be a reliable means of separating the species. A better distinction is that the band along the hind margin of the pronotum is brown towards the centre in *G. vernale* (fig. 3V) but black along the whole length in *G. boltoni* (fig. 3B). Also the front edge of the fronto-clypeus is angled in the middle in *G. vernale* (fig. 2V) and uniformly rounded in *G. boltoni* (fig. 2B).

Glossosoma intermedia (Klapálek).

Material: Hayes Water inflow CU, 3 cast skins ; Hoathwaite Beck WL, 3 whole larvae ; R. Troutbeck WL, 2 whole larvae.

Larvae and cases about the same size as those of the two preceding species.

Kimmins (1943), in his description of this species, noted a difference in the shape of the mandible, but this was probably due to wear as found in the other species. He also noted, on the terminal abdominal hook, two bristles, not shown in Lestage's drawing of *G. boltoni*. But, in fact, their absence in the illustration was probably an error, for they are present on all the specimens of *Glossosoma* that have been examined.

Front edge of fronto-clypeus (fig. 2M) like that of *G. vernale*. Posterior edge of pronotum brown towards the centre, as in *G. vernale*. The distinguishing character of this species is that the dark spot on the side of the pronotum, just above the place of attachment of the first pair of legs, is smaller than in the two preceding species (fig. 3M).

Agapetus fuscipes Curtis.

Material: Ford Wood Beck WL, 1 cast skin, 10 whole larvae ; Wilfin Beck WL, 8 cast skins ; Malham Tarn inflow MY, 2 cast skins ; small stream at Porth Clais PB, 1 cast skin ; Coulton Beck WL, 1 cast skin ; R. Leven WL, 2 cast skins ; R. Brathay WL, 1 cast skin.

Larvae from 4 to 7 mm. long when fully grown. Stone cases about the same length.

Head varies in colour in different specimens from light to dark brown. Anterior edge of fronto-clypeus concave and slightly V-shaped.

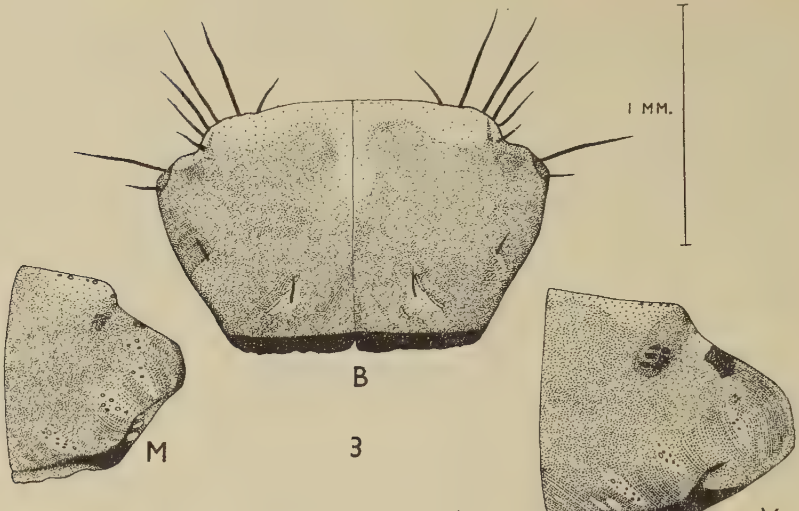
Pronotum (fig. 5*f*) bordered anteriorly with a double row of long black setae, and there is a dark band along the posterior border. A mark on the side of the pronotum is barely visible. Sclerotised patches present on meso- and metanotum, as shown in fig. 5*f*, these patches being very conspicuous on fully grown larvae.

Legs robust and all of about equal length. Each claw bears on its inner surface, a single seta arising from a very short footstalk (fig. 4*f*). Abdomen creamy-yellow ; each segment with numerous long hairs ventrally and dorsally. Anal claw short and robust, and has, attached to the outer surface, two and occasionally three auxiliary spines.

A. delicatulus McLachlan.

Material: Hayes Water inflow CU, 3 cast skins, 1 whole larva ; R. Wharf MY, 3 cast skins ; R. Clyde LA, 3 cast skins ; R. Troutbeck WL, 1 cast skin ; R. Bela WL, 1 cast skin ; R. Eden CU, 1 cast skin.

This species differs from the foregoing in three main characters. Fore margin of fronto-clypeus evenly rounded ; this distinction is clear on mounted cast skins. The marking on



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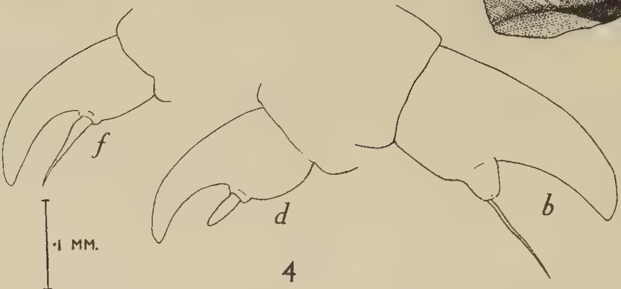

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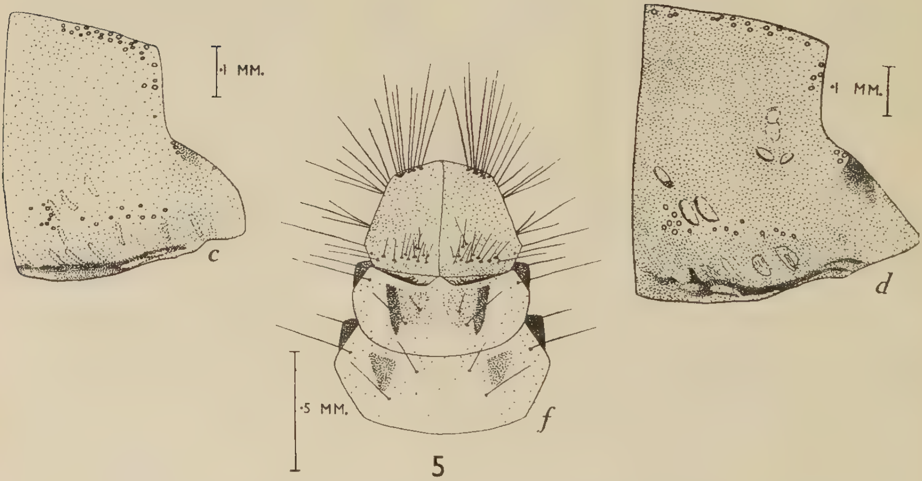

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FIG. 3.—Pronota: B, *Glossosoma boltoni*, drawn from whole larva; M, *G. intermedia*; V, *G. vernale*, both drawn after half the pronotum was pressed out flat.

FIG. 4.—Claws: *f*, *Agapetus fuscipes*; *d*, *A. delicatulus*; *b*, *G. boltoni*.

FIG. 5.—*f*, Dorsal view of thorax of *Agapetus fuscipes*; *c*, Pronotum of *A. comatus*; *d*, Pronotum of *A. delicatulus*.

the side of the pronotum just over the point of insertion of the fore leg dark and conspicuous, as shown in fig. 5*d*. This character is best seen if the pronotum is removed and squashed flat. Sclerites on the metanotum small and rounded.

A. comatus (Pictet).

Material : R. Wharfe MY, 1 cast skin ; R. Wey SR, 1 cast skin, 6 whole larvae.

This species can be distinguished from *A. delicatulus* by the dot on the side of the pronotum being pale and inconspicuous (fig. 5*c*) and from *A. fuscipes* by the sclerites on the metanotum being small and round.

NOTES ON OCCURRENCE AND FLIGHT-PERIOD OF THE SPECIES.

All the records of *G. boltoni* are from streams and small rivers, with adults emerging from mid June to late August. *G. vernale*, to judge from the published records, is found mainly in larger rivers, with adults emerging from mid April until late September. *G. intermedia* is known from three localities only. In two of these, larvae have been found over-wintering in their pupal cases, but the time of emergence was not discovered. In the third adults emerged in March. *A. fuscipes* is widespread and larvae have been recorded from streams, rivers and lakes, with adults emerging from May to August. *A. comatus* has been recorded only from rivers, with adult records from late May to early August. *A. delicatulus* larvae have been collected from both streams and rivers. The adults emerge in August. There are some southern records of adults in July.

CU = Cumberland, LA = Lanark, MY = Mid Yorkshire,
PB = Pembrokeshire, SR = Surrey, WL = Westmorland.

ACKNOWLEDGMENTS.

I am indebted to Dr. T. T. Macan for helpful advice during this work, and to Mr. D. E. Kimmins of the British Museum for identifying some of the adults.

KEY TO THE FULLY GROWN LARVAE.

1 Larvae 8 to 10 mm. in length. Single row of long black setae along the anterior edge of the pronotum (fig. 3B). No sclerotised patches on the meso- or metanotum. Seta on inner surface of claw arising from a footstalk (fig. 4*b*). Anal claw with a single auxiliary spine attached to the outer surface . . . . **Glossosoma** 2

– Larvae 4 to 7 mm. in length. Double row of long black setae along anterior edge of pronotum (fig. 5*f*). Sclerotised patches present on both meso- and metanotum. Seta on inner surface of claw arising from a very short footstalk (figs. 4*f* and *d*). Anal claw generally with 2 or 3 auxiliary spines attached to the outer surface . **Agapetus** 4

2 Spot on side of pronotum small (fig. 3M) . . . . **G. intermedia**

– Spot on side of pronotum large (fig. 3V) 3

3 Posterior edge of pronotum entirely black (fig. 3B). Front margin of fronto-clypeus uniformly rounded (fig. 2B) . . . . **G. boltoni**

– Posterior edge of pronotum brown towards centre (fig. 3V). Front margin of fronto-clypeus angled in the middle (fig. 2V) . . . **G. vernale**

4 Sclerites on metanotum larger (fig. 5*f*) ; setae on claws long (fig. 4*f*) **A. fuscipes**
– Sclerites on metanotum smaller ; setae on claws short (fig. 4*d*) . . . 5
5 Spot on side of pronotum dark and conspicuous (fig. 5*d*) . . **A. delicatulus**
– Spot on side of pronotum light brown and smaller (fig. 5*c*) . . **A. comatus**

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RAINFALL AND LARVAL DENSITY OF *CULICOIDES IMPUNCTATUS* GOETGHEBUER (DIPTERA : CERATOPOGONIDAE).

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During the last three years (1953–6) experiments have been conducted on Soutra Hill, Midlothian, to find a suitable insecticidal preparation for use against the larvae of *Culicoides impunctatus* Goet. The results of these experiments, the methods employed and a description of the area have already been given in Kettle, Nash and Hopkins (1956) and Kettle and Parish (*in the press*). In the preparation of the second of these papers attention was drawn to the importance of rainfall on larval control and it was noticed that there appeared to be a close relationship between rainfall and larval density. This observation forms the subject of the present note.

In the control study it was necessary to follow natural fluctuations in the larval population by sampling untreated plots. Five of these (three from Site I and two from Site II) were sampled for three consecutive years. On each occasion nine 3-inch diameter samples were removed from each plot, making a total of 45 samples with an area of 2·2 sq. ft.

The samples were taken in the autumn, except for the first sampling of the two plots on Site II which was made in March 1954. For convenience they have been included in Table I, with the autumn 1953 samples from Site I.

Table I.—*Relationship between rainfall and larval density of* C. impunctatus. *Rainfall measured at the Royal Observatory, Edinburgh, during the period of adult activity, i.e. May to September inclusive. Larval density on Soutra Hill, Midlothian, given as total larvae in* 45 *three-inch diameter samples* (= 2·2 *sq. ft.*)

Year.	Rainfall May–Sept. inclusive (inches).	Larval density.		
		Actual, in autumn.	Calculated.	Difference.
1953	12·56	141	144	+3
1954	17·24	287	282	−5
1955	6·67	69	69	0

It is common knowledge that the man-biting midge, *C. impunctatus*, is particularly troublesome on the West Coast of Scotland and in the Western Isles. It is also widely appreciated that these areas are among the wettest in Britain, but, however, the relationship between rainfall and *C. impunctatus* is complex. *C. impunctatus* larvae are to be found in bogland sites covered with *Sphagnum* and *Polytrichum* (Kettle and Lawson, 1952). The maintenance and very existence of these breeding sites depends on a high rainfall, i.e. the precipitation/evaporation (P/E) ratio should exceed unity. For the larvae to survive, the peat must be kept moist by intermittent rainfall. Under conditions of prolonged drought, particularly if accompanied by high temperature, the peat may dry out and the larvae die. Such an event occurred on Loch Lomondside in the summer of 1949 (Kettle, 1950) where the peat formed a shallow layer on top of boulder clay and was therefore susceptible to drying out.

Presumably female *C. impunctatus* will not oviposit on dry peat so that the rainfall during the period of adult activity (May to September inclusive) will limit the number of suitable oviposition sites. In addition high humidity, which depends to some extent upon rainfall, will prolong the length of adult life and ensure that more females successfully mature batches of eggs. It seems likely, therefore, that rainfall will exert its greatest effect on *C. impunctatus* during the period May to September, and in the following analysis this will be referred to as " summer rainfall ". In British Meteorology the term " summer rainfall " covers the six months period April to September.

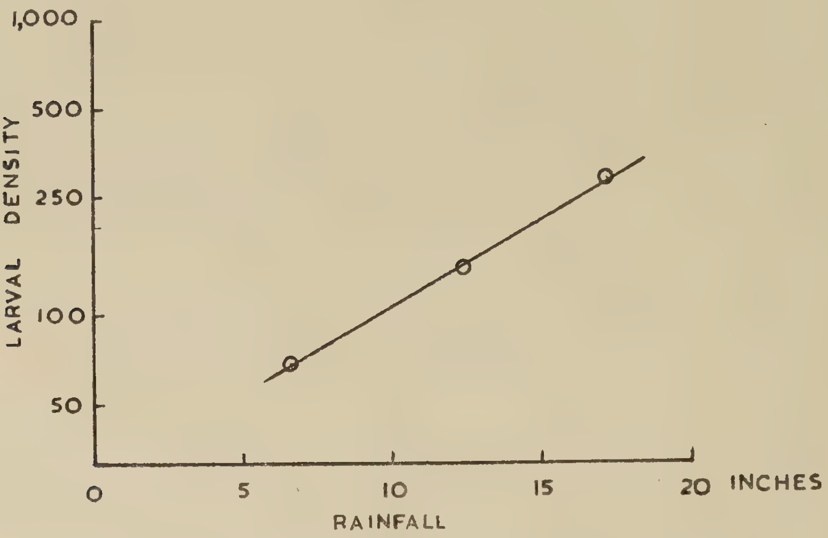

Fig. 1.—Rainfall and larval density of *C. impunctatus* on Soutra Hill. (For details see Table I.)

As there is no meteorological station close to Soutra Hill, I have used the records of the Royal Observatory, Edinburgh, which is 15 miles North-west of Soutra. These were made available through the courtesy of the Meteorological Office, Edinburgh. A rainfall map of Great Britain published by Director General, Ordnance Survey 1949, gives the average annual rainfall in the years 1881–1915. On this the Royal Observatory appears to have an annual rainfall of 27·5 inches and Soutra Hill of 35 inches. Therefore, it is necessary to increase the readings at the Royal Observatory by 25 per cent. to give likely figures for Soutra Hill.

In Table I and figure 1 the larval density of *C. impunctatus* on Soutra Hill has been plotted against the rainfall measured at the Royal Observatory in the preceding May to September. There is surprisingly close positive correlation between the two variables. The relationship can be expressed in the form :

$$\log y = 0{\cdot}058\, x_e + 1{\cdot}450 \tag{1}$$

where

x_e = rainfall in inches at the Royal Observatory

and

y = *C. impunctatus* larval density on Soutra Hill

The effect of correcting for the greater rainfall on Soutra Hill is to increase the value of x_e by 25 per cent. (× 5/4). To compensate for this change the value of the slope or regression (0·058) must be reduced by one-fifth (× 4/5). The equation now reads

$$\log y = 0{\cdot}046\, x_5 + 1{\cdot}450 \tag{2}$$

where

x_5 = probable rainfall in inches on Soutra Hill

and

y = larval density on Soutra Hill.

It will be noticed that, when there is no summer rainfall ($x = 0$), the larval density should be 28 (i.e. $\log y = 1{\cdot}450$), but it must be remembered that this is assessed not by taking samples at random, but by sampling from suitably vegetated areas. In fact, when there is regularly no rainfall in the summer, there will be no suitably vegetated area to sample. In all probability the rainfall on Soutra Hill and in the East of Scotland as a whole is approaching the lower limit for the survival of *C. impunctatus*, areas of *Sphagnum* and *Polytrichum* being restricted to the higher ground in this region. The overriding importance of rainfall in the survival of the midge is indicated by the closeness of the correlation between rainfall and larval density.

From equation 2 it would seem that the larval density should double for every 6·5 inches more rain in the summer. It is likely, however, that in the West of Scotland and other very wet regions rainfall may cease to be the critical factor limiting the size of the midge population, and be replaced by another.

It would be interesting to know the " normal " larval density on Soutra Hill. The average rainfall at the Royal Observatory for the months of May to September during the period 1896–1930 was 12·13 inches. This is almost the figure (12·56) obtained in 1953, but 1954 was much wetter than usual (17·24) and 1955 much drier (6·67).

The reduction in larval density brought about by the drought of 1955 was achieved partly by reducing the available breeding area, and partly by reducing the adult longevity. Thus three of the five plots under observation—2 on Site I and 1 on Site 2—almost ceased to breed. They yielded only 6 larvae compared with 66 in 1953, an " average " year. On the other two plots the reduction was much less—63 compared to 75 larvae. There was, therefore, both a reduction in the area still breeding and within this a reduction in the larval density. This implies that either less eggs were laid, i.e. fewer females survived long enough to mature a batch of eggs, or the proportions of eggs which hatched and/or larvae which survived were reduced.

The values of summer rainfall would be more useful if they were converted into figures of annual rainfall. The average annual rainfall at The Royal Observatory for 1896–1930 was 26·31 inches, of which 12·13 inches or 46 per cent. fell in the months of May to September. In 1953, 1954 and 1955 the percentages of the annual rainfall which fell during May to September were 53 per cent., 49 per cent. and 37 per cent. and over the three years the percentage was 47. The summer rainfall can be obtained by dividing the annual rainfall by a factor of 2·17 (= annual rainfall/summer rainfall).

Unfortunately the same factor is not applicable to all areas. Bilham (1938 : 87, fig. 28) gives the percentage summer rainfalls for North, East and West Scotland as 32·6 per cent., 40·5 per cent. and 36·4 per cent. respectively and the corresponding factors will be 3·07, 2·47 and 2·75.

Buchan (1892) published rainfall data for many Scottish stations for the years 1866–1890. In grouping his data I have confined myself to those stations in which there is a complete record for the twenty-five years involved. The results of this are given in Table II. If the rainfall were equally distributed throughout the year then five-twelfths, or 42 per cent., would fall during May to September. It will be noted that Orkney and Shetland have the lowest percentage summer rainfall with 33 per cent. and a factor of 3·02. The percentage is a little higher in West and Central Scotland, varying from 34 to 37 per cent., with factors of 2·67–2·95, while in the East of Scotland the percentages vary from 40–44 per cent. and the factors from 2·29–2·53, the lowest factor being that of the Lothians in which both Soutra and the Royal Observatory are situated.

TABLE II.—*Annual and summer rainfall in various regions of Scotland, with summer rainfall as a percentage of annual and the ratio of annual/summer rainfall. Data from Buchan* (1892) *for years* 1866–1890.

Region.	Counties.	Number of Stations.	(a) Annual rainfall.	(b) Rainfall May to September.	(c) (b) as % of (a).	(d) Factor (a)/(b).
Northern .	Orkney ; Shetland	8	33·29	11·02	33	3·02
Western .	Hebrides	9	49·80	16·84	34	2·95
,, .	W. Ross ; W. Inverness	3	44·27	15·56	35	2·84
,, .	Argyll ; Bute	14	51·31	18·59	36	2·76
,, .	Ayr ; Renfrew ; Lanark	13	45·35	16·97	37	2·67
,, .	Dumfries ; Kirkcudbright	7	42·21	15·21	36	2·77
Central .	Dunbarton ; Stirling	6	55·82	20·85	37	2·68
,, .	Perth	13	61·93	22·26	36	2·78
Eastern .	Caithness ; E. Ross ; E. Sutherland ; E. Inverness	8	29·86	11·80	40	2·53
,, .	Angus ; Aberdeen ; Kincardine ; Nairn; Moray; Banff	21	31·63	13·30	42	2·38
,, .	Fife ; Kinross ; Clackmannan	4	36·54	15·14	41	2·41
,, .	Lothians	13	30·85	13·45	44	2·29
,, .	Peebles ; Roxburgh ; Selkirk ; Berwick	11	34·65	14·12	41	2·45

The average summer rainfall at the Royal Observatory is 12 inches. As the rainfall on Soutra is about 25 per cent. more, its average summer rainfall will be 15 inches. Using the factor of 2·41, which is applicable to the East of Scotland, this represents an annual rainfall of 36·1 inches (15 × 2·41). In western and central Scotland a summer rainfall of 15 inches is equivalent to an annual rainfall of 41·3 inches. From the point of view of *C. impunctatus* there is nothing to choose between an annual rainfall of 36 inches in East Scotland and 41 inches in West Scotland.

It is comforting to realise that the degree of control attained by larvicides is also dependent upon rainfall (Kettle and Parish (*in the press*)), so that higher rainfall not only increases the larval density but also greatly increases the efficiency of any larvicide.

SUMMARY.

In the course of regular observation on the larval population of *Culicoides impunctatus* on Soutra Hill, Midlothian, it was found that there was a close correlation between larval density in the autumn and the rainfall during the preceding period of adult activity, i.e. May to September. The ratio between the " summer " rainfall and the annual rainfall is given for various regions of Scotland.

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